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TABLE OF CONTENTS

A FOURTH TYPE OF NODAL ANATOMY IN DICOTYLEDONS, ILLUSTRATED BY CLERODENDRON TRICHOTOMUM THUNB. With one plate. By Margery P. F. Marsden and I. W. Bailey	1
A MONOGRAPH OF THE GENUS PHILADELPHUS (Continued). By Shiu-ying Hu	52
INDUCTION OF EARLY FLOWERING OF ORNAMENTAL APPLE TREES. By Karl Sax and Albert G. Johnson	110
RHODODENDRON MACROPHYLLUM D. DON EX G. DON. By Leonard F. Frisbie	115
DEDICATION [IRVING WIDMER BAILEY]. With portrait	i
THE COMPARATIVE MORPHOLOGY AND RELATIONSHIPS OF THE MAGNOLIACEAE—IV. WOOD AND NODAL ANATOMY. With three plates. By James E. Canright	119
THE TAXONOMIC USE OF SPECIALIZATION OF VESSELS IN THE METAXYLEM OF GRAMINEAE, CYPERACEAE, JUNCACEAE, AND RESTIONACEAE. With one plate. By Vernon I. Cheadle	141
THE POLLEN MORPHOLOGY OF SEVERAL GENERA EXCLUDED FROM THE FAMILY ICACINACEAE. With one plate. By A. Orville Dahl	159
THE SEED AND GINKGO. By Arthur J. Eames	165
SOME FACTORS IN POLLEN GERMINATION: CALCIUM SALTS, DEXTROSE, DRYING. By Anna F. Faull	171
COMPARATIVE MORPHOLOGY OF THE FOLIAR SCLEREIDS IN BORONELLA BAILL. With five plates. By Adriance S. Foster	189
A TAXONOMIC REVISION OF PODOCARPUS. IX. THE SOUTH PACIFIC SPECIES OF SECTION EUPODOCARPUS, SUBSECTION F. With one plate. By Netta E. Gray	199
THE VEGETATION OF BEATA AND ALTA VELA ISLANDS, HISPANIOLA. With five plates. By Richard A. Howard	209
ON THE PRIMARY VASCULAR SYSTEM AND THE NODAL ANATOMY OF EPHEDRA. With three plates. By Margery P. F. Marsden and Taylor A. Steeves	241
THE OCCURRENCE OF EUPTELEA IN THE CENOZOIC OF WESTERN NORTH AMERICA. With three plates. By Richard A. Scott and Elso S. Barghoorn	259
STALK DIAMETER AS A FACTOR IN FRUIT SIZE. By Edmund W. Sinnott	267
PHANEROGAM GENERA WITH DISTRIBUTIONS TERMINATING IN FIJI. By A. C. Smith	273

MITOCHONDRIA AND PRECIPITATES OF A-TYPE VACUOLES IN PLANT CELLS. With three plates. By <i>Helen P. Sorokin</i>	293
ON THE DIFFERENTIATION OF XYLEM. With six plates. By <i>Ralph H. Wetmore and Sergei Sorokin</i>	305
A MONOGRAPH OF THE GENUS PHILADELPHUS (Continued). By <i>Shiu-ying Hu</i>	325
STUDIES ON THE PROGENY OF TRIPLOID PHILADELPHUS AND FORSYTHIA. With one plate. By <i>Dexter R. Sampson</i>	369
GEOGRAPHICAL DISTRIBUTION OF THE EUPOMATIACEAE. By <i>A. T. Hotchkiss</i>	385
FURTHER NOTES ON THE WEEDS AND INTRODUCED PLANTS OF FIJI. By <i>William Greenwood</i>	397
THE DIRECTOR'S REPORT	403
BIBLIOGRAPHY OF THE PUBLISHED WRITINGS OF THE STAFF AND STUDENTS, July 1, 1954—June 30, 1955	428
STAFF OF THE ARNOLD ARBORETUM, 1954—1955	431
INDEX TO VOL. XXXVI	433
TITLE-PAGE AND TABLE OF CONTENTS	i—iv

VOLUME XXXVI

NUMBER 1

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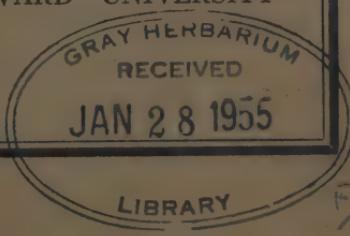
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CONTENTS OF NO. 1

A FOURTH TYPE OF NODAL ANATOMY IN DICOTYLEDONS, ILLUSTRATED BY CLERODENDRON TRICHOTOMUM THUNB. With one plate. By <i>Margery P. F. Marsden and I. W. Bailey</i>	1
A MONOGRAPH OF THE GENUS PHILADELPHUS (Continued). By <i>Shiu-ying Hu</i>	52
INDUCTION OF EARLY FLOWERING OF ORNAMENTAL APPLE TREES. By <i>Karl Sax and Albert G. Johnson</i>	110
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NUMBER 1

A FOURTH TYPE OF NODAL ANATOMY IN DICOTYLEDONS,
ILLUSTRATED BY CLERODENDRON TRICHOTOMUM THUNB.

MARGERY P. F. MARSDEN * AND I. W. BAILEY

With one plate and seventeen figures

INTRODUCTION

IN 1914, Sinnott demonstrated by an analysis of 34 orders and 164 families that there are three significant forms of foliar nodal anatomy in dicotyledons, viz. (1) the *unilacunar* form in which the vascular supply of the leaf is related to a single gap in the stele, (2) the *trilacunar* form in which the vascular strands are related to three distinct and more or less widely separated gaps, and (3) the *multilacunar* form in which five or more vascular strands are related to as many independent gaps. Although various dicotyledonous families are prevailingly unilacunar, trilacunar or multilacunar — thus providing significant evidence in the identification and classification of plants — there is a considerable number of families and many orders in which transitions between the different forms of nodal anatomy occur. Sinnott concluded that the trilacunar condition is primitive in angiosperms, the multilacunar form (much modified in monocotyledons) having arisen by amplification of the number of independently attached lateral strands, and the unilacunar form (a) in certain families by reduction and elimination of the two lateral strands and (b) in other families by the approximation of the median and lateral strands forming an aggregation of three strands that is related to a single gap in the stele.

Using this conclusion as a basis, Sinnott and Bailey (1914, 1915) attempted to demonstrate by statistical correlations that the primitive angiospermic leaf was simple and palmately veined. Subsequently, Eames (1931) adopted the concept of a primitive trilacunar condition as a working hypothesis in the study of floral morphology. Thus, nodal anatomy became part of the foundation for considerable phylogenetic investigation.

Recently, studies of the Austrobaileyaceae (Bailey and Swamy, 1949),

* This investigation was supported in part by a fellowship from the English-Speaking Union, and by the Fanny Bullock Workman Fellowship from Radcliffe College. Part of this paper represents a portion of a thesis submitted for the Ph.D. degree in Radcliffe College to the Department of Biology, Harvard University.

Monimiaceae (Money, Bailey and Swamy, 1950) and Chloranthaceae (Swamy and Bailey, 1950; Swamy, 1953a) have revealed patterns of foliar vasculature which necessitate a comprehensive reassessment of the significance of nodal anatomy in the phylogeny of the angiosperms.

The leaves of the majority of dicotyledons, as indicated by Sinnott, are vascularized by what appears at the nodal level to be an odd number (1, 3, 5, 7, etc.) of discrete vascular strands. On the contrary, the leaves of *Austrobaileya*, *Trimenia*, and *Ascarina* are vascularized by two independent strands that are related to a single gap at the nodal level. Since similar structures occur in various gymnosperms and in the cotyledonary node of many dicotyledons, it is essential to determine whether the foliar unilacunar nodes of dicotyledons have been derived in all cases from a trilacunar one.

Most of the work in the past has dealt with comparative investigations of fully matured structures at nodal levels. Such comparative studies of end-products without comprehensive developmental investigations at successive levels of the shoot and leaf, may be misleading. What is needed in the study of the evolution of various plant organs, as well as of the plants as a whole, is "a phylogeny of successively modified ontogenies." Therefore it is essential to obtain an accurate developmental picture of plants which have a double leaf trace at their unilacunar nodes. Being unable to obtain viable seeds of such ranalian genera as *Austrobaileya*, *Trimenia* and *Ascarina*, it seemed desirable to make a comprehensive study of the vascularization of *Clerodendron trichotomum* Thunb. of the Verbenaceae, which has at maturity a similar type of nodal anatomy.

MATERIAL AND METHODS

Adult plant: Abundant material was obtained from shrubs of *Clerodendron trichotomum* Thunb. in the Rare Plants section of the Arnold Arboretum. Weekly collections of buds, nodal material, and young and mature leaves were made from March 20 to about September 15, 1952, and after this, collections of buds were made irregularly until March, 1953.

The morphology of *C. trichotomum* has been described by Lam (1919). The material used for our studies, however, does not completely agree with his description, since the three-lobed leaves which he records have never been observed in adult specimens, but large-lobed juvenile leaves have been observed on two-year-old plants grown from seed. Specimens of the plants used in these investigations have been placed in the herbarium of the Arnold Arboretum.

The plants of *C. trichotomum* are shrubs 8 to 10 ft. in height, which branch profusely, particularly from the base of the main stem. The leaves are arranged in an opposite and decussate manner; they are simple, lanceolate to ovate, slightly serrate and have reticulate venation. The lamina of adult leaves is approximately 8 cm. long, while that of the juvenile ones is approximately 12 cm. long. The petioles are frequently as long as the leaves.

In the axil of each leaf there is a lateral bud complex. This consists of one main bud with one pair of subsidiary buds, lateral to it, and usually one additional sub-lateral bud. From these aggregations of buds lateral branching often occurs near the base of the shoot, in one- and two-year-old plants.

The inflorescence is a many-flowered cymous panicle, and is trichotomous. Each of the lateral cymes arises in the axil of a foliage leaf. Reduced scale-like bracts subtend the higher divisions of the inflorescence; these are caducous.

Seedling: Originally, supposedly fresh seed of *C. trichotomum* was obtained through a commercial seed house. Some of this seed was planted in seed pans in the greenhouses of the Biological Laboratories, Harvard University. Other samples of the same seed were presoaked, scarified, or given cold treatment at 5 degrees C. in moist peat for 6-8 weeks to allow after ripening. In all cases germination occurred in less than 3% of the seeds planted.

The next fall ripe fruits were collected directly from the shrubs in the Arnold Arboretum. The seeds were removed, immediately planted on the surface of soil, and covered by damp sphagnum moss. They were planted in mid-October and were kept in the greenhouses of the Arboretum. By mid-December approximately 10% of the seeds planted had germinated. Germination continued until by mid-January approximately 70% of the seeds had germinated.

There appears to be no description of the fruit, seed, or seedling of *C. trichotomum* in the literature, although the seed and seedling of *C. Kaempferi*, Fisch. has been described by Lubbock (1892). This description differs so markedly from *C. trichotomum* (probably because Lubbock failed to recognize that *C. Kaempferi* is hypogeal in germination) that the following description of *C. trichotomum* is given here.

The fruit is formed from a gynoecium which consists typically of four carpels. There is a single loculus and each carpel usually bears two ovules; however, in the fruit there are never more than four seeds and frequently only two or three. Each seed has an extremely hard and sclerotic testa which is sculptured on one side, and smooth with a deep longitudinal groove on the other side. Through this groove the fleshy funicle attaches the seed to the placenta. On germination the radicle emerges through this longitudinal groove, which also marks the line of weakness along which the testa eventually splits. The seed is non-endospermic and the cotyledons are large and fleshy.

Germination is hypogeal (see PLATE I:3). Shortly after the radicle emerges through the longitudinal slit, the shoot appears above the surface of the ground with its tip bent over (PLATE I:3c, d). The epicotyl straightens, elongates and carries the first pair of leaves upwards (PLATE I:e, f). The fleshy cotyledons remain underground enclosed in the testa; after about three months they shrivel and become detached.

The hypocotyl is minute, 2-3 mm. long, 2 mm. thick, and glabrous. The epicotyl (i.e., between the point of attachment of the cotyledons and the

first pair of leaves) is 4.5–6 cm. long, pale green and pubescent. The cotyledons are stalked (petiole 3–5 mm. long, lamina 8–10 mm. long), white, fleshy, ovate, entire, without obvious venation; they are enclosed in the testa. The root is a tap root bearing many lateral branches. The first internode of the stem is 4.25–6 cm. long, the second 2–3 cm. long and subsequent internodes are 1 cm. long or less. The stem is cylindrical, bright green, pubescent. The leaves are simple, opposite and decussate, exstipulate and petiolate. The petiole is very long; the lamina and petiole are pubescent on both surfaces. Leaves at the first node are suborbicular, pale green, larger than the cotyledons with margins irregularly toothed towards the apex. At the second node leaves are rhomboidal to ovate and the margins are irregularly toothed. The third pair of leaves resembles the adult leaves which are ovate and irregularly toothed.

Histological techniques: Seedling, foliar and nodal material was fixed in formal acetic alcohol, medium chromo-acetic and strong chromo-acetic alcohol (Johansen, 1940). A modified Zirkle's n-butyl alcohol method for dehydrating refractory plant material was employed and subsequently the paraffin-tissuemat method described by Pratt and Wetmore (1951) was used for embedding the material. Hard tissues were presoaked in water before sectioning. Embedded material was sectioned on a Spencer rotary microtome at 8 to 10 micra. Egg albumen fixative was used for mounting the serial sections, and preparatory to staining the slides were coated with a $\frac{1}{2}\%$ solution of parloidion in ether.

Staining combinations used for serial sections were as follows: — Heidenhain's iron-alum haematoxylin with safranin as a counterstain (Jeffrey, 1917); 1% safranin counterstained with picro-aniline blue (1 gm. water soluble aniline blue to 100 cc. of 80% ethyl alcohol with 1 cc. of saturated aqueous picric acid); 1% safranin and a saturated solution of cotton blue in lactophenol. In very young material where it was desired to emphasize meristematic tissues, as for example in seed and seedling sections, Foster's (1934) tannic acid and ferric chloride technique was employed.

Foliar material was cleared by use of a 5–8% NaOH solution (Bailey and Nast, 1943). In the case of seedling material, clearing methods involving the use of lactic acid (Debenham, 1939) have been found to be more satisfactory than the NaOH method. A basic fuchsin stain was used in some cases to accentuate the vascular pattern (De Tomasi, 1936; Kumar et al., 1942).

VASCULARIZATION OF SEED AND SEEDLING

Seed: Seed obtained directly from shrubs in October was examined by means of serial sections since the fleshy cotyledons are difficult to clear without damage to the delicate epicotyl and radicle. At the cotyledonary node each cotyledon possesses two distinct procambial¹ strands (FIG. 1:A). Four vascular strands differentiate behind the shoot apical meristem as it

¹ The criteria used by Esau (1942, 1943a, and 1943b) for the identification of the procambium, first-formed xylem, and first-formed phloem have been followed in this investigation.

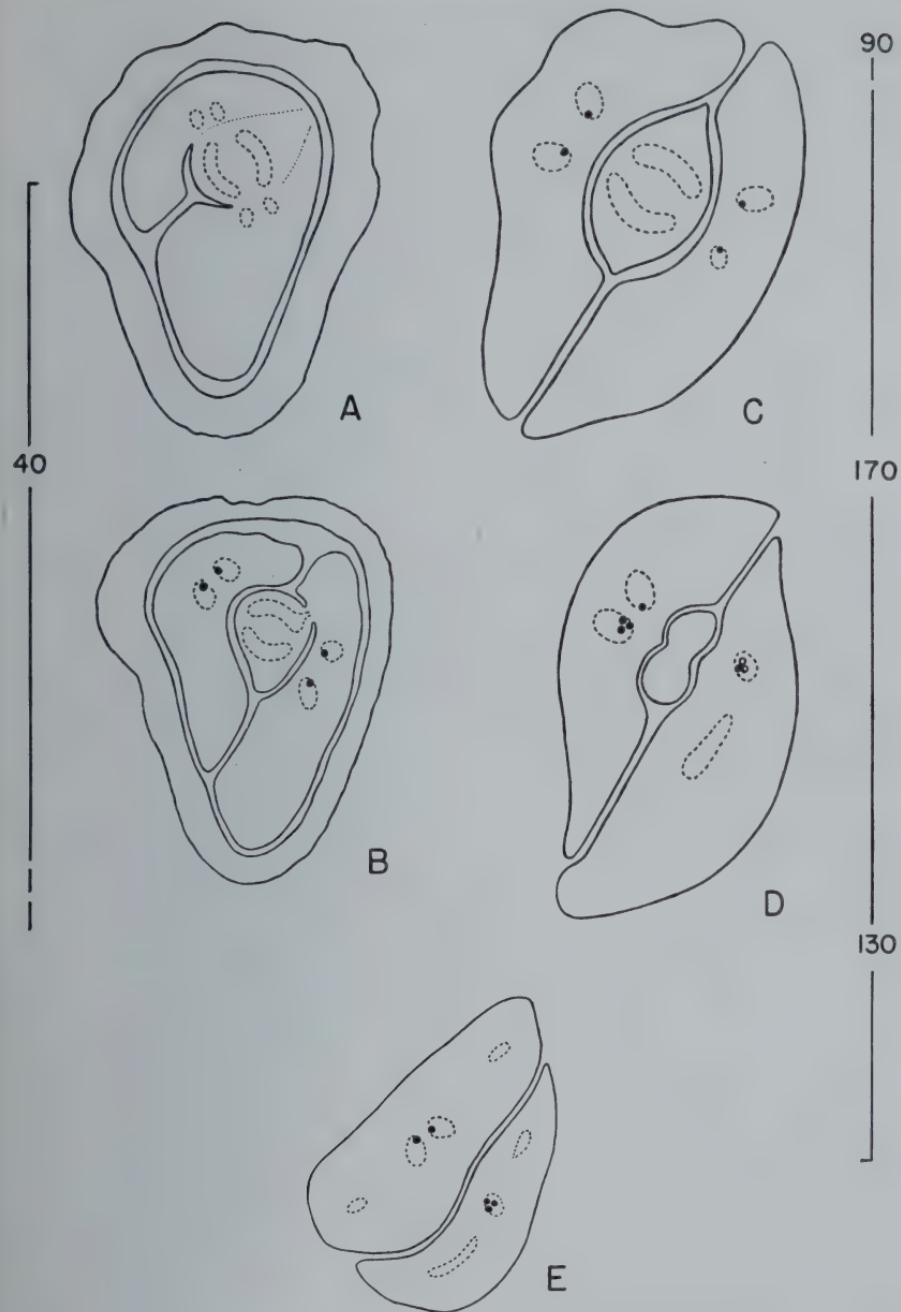


FIGURE 1

SERIES OF SECTIONS OF THE SEED OF *Clerodendron trichotomum*. Procambium is represented within the dotted lines, and first xylem elements as black dots. The distance in micra between sections is shown on the left and right.

elongates but at this early stage these are not obvious and the procambium has the appearance of an indistinct cylinder. The procambium of the root forms a solid central core.

At the cotyledonary node the procambial cylinder forms two arcs (FIG. 1:A); the gaps in the procambial cylinder occur at the points of attachment of the two cotyledons. At this stage there is no differentiation of xylem in the epicotyl, in the cotyledonary node nor in the bases of the cotyledons. In the radicle, which is much larger and better developed than the shoot, four spiral or annular xylem elements differentiate about 800 micra below the cotyledonary node in the position of the protoxylem points of a tetrach root.

Approximately 50 micra above the cotyledonary node two protoxylem elements differentiate in each cotyledon, one in each of the procambial groups (FIG. 1:B). At a distance of 100 micra above the cotyledonary node additional elements appear in the procambial strands of the cotyledons, and between 100 and 250 micra each may possess as many as three parallel xylem elements (FIG. 1:D). At this level, and above, lateral procambial strands depart so that the entire vascular pattern of each cotyledon is laid out (FIG. 1:E). Between 250 and 300 micra, however, differentiation is less, until finally at 350 micra no protoxylem elements can be observed, although the procambial strands remain distinct.

First seedling stage: Approximately two months after the seeds have been planted the radicle emerges from the longitudinal slit in the testa. Seedlings which are examined at this stage when the radicle is only a few millimeters long (PLATE I:3b) show that the differentiating xylem in the cotyledons links with that in the root. The shoot, which has grown very little, still possesses a distinct procambial pattern but shows no differentiation of first-formed xylem. Two distinct xylem groups are present in each cotyledon well above the cotyledonary node and these differentiate acropetally towards the tip of the cotyledon and basipetally towards the cotyledonary node. The two procambial strands in each cotyledon may remain distinct for its entire length, or, as is more usual, they coalesce towards the tip of the cotyledon. Similarly the differentiating xylem remains distinct for some considerable distance, but towards the tip there is usually a single spiral first-formed xylem element. At about 400 micra from the cotyledonary node the maximum number of xylem elements is observed, and here there are two distinct first-formed xylem elements which are usually spiral in thickening and which are located towards the inside of each of the procambial groups. Two or three late-formed primary xylem elements may also differentiate at this level in the cotyledons and development is centrifugal towards the margin of the cotyledon.

Later differentiation between the region of initial maturation in the cotyledons and the cotyledonary node is basipetal. Frequently the newly formed xylem nearer the cotyledonary node is scalariform and therefore probably "late formed primary xylem."² Spiral and annular xylem ele-

² It is well known that the term protoxylem is used to denote the first-formed xylem in plants, and that although this frequently exhibits spiral and annular thickening

ments always drop out of the cotyledonary traces as they are followed downwards through the node.

The *transition region* of a very young seedling before epicotyl elongation exhibits much the same form as that in an older seedling where the shoot becomes vascularized. The procambium in the epicotyl is divided into four distinct strands (FIG. 2:1). At the cotyledonary node each trace from the cotyledons passes in towards a separate procambial strand from the epicotyl (FIG. 2:2) and joins with it (FIG. 2:2). Below the cotyledonary node the four partially differentiated vascular bundles remain distinct; if any protoxylem is present the arrangement is endarch. Between 300 and 700 micra below the cotyledonary node any spiral or annular xylem related to the cotyledonary traces drops out, and four distinct annular xylem elements appear in the position of the protoxylem poles of the root, i.e., in the gaps between the vascular bundles of the hypocotyl (FIG. 2:4, 5, 6). These protoxylem traces are in no way connected with the cotyledonary traces but extend upwards from the protoxylem points of the root protostele. They usually extend farther up in the gaps at right angles to the median axis of the cotyledons than in the gaps between the two traces of each cotyledon (FIG. 2:5).

At the cotyledonary node the phloem lies on the same radius as the meta- and protoxylem and remains in the same position throughout the hypocotyl and into the root. In the hypocotyl the internal annular elements along this radius drop out, leaving collateral bundles of phloem and scalariform xylem (FIG. 2:4-7). Passing downwards these bundles approach each other about the center of the axis until a solid xylem core is formed surrounded by the same four strands of phloem (FIG. 2:7, 8). Meanwhile new protoxylem strands have appeared along radii alternate with the collateral bundles (FIG. 3); these become the protoxylem poles of the tetrach root (FIG. 2:8). Hence the first-formed xylem of the shoot is not continuous with that of the root, but joins with metaxylem from the root at a level in the hypocotyl at which protoxylem strands from the root protoxylem poles have already been differentiated. This fact is illustrated in figures 2 and 3.

It is quite obvious that the transformation of vascular pattern from the true root to true stem condition described for *Clerodendron trichotomum* in no way corresponds to the "transition types" postulated by Van Tieghem (1891); nor has any twisting, rotation or inversion been observed such as is described by Eames and MacDaniels (1947), Lenoir (1920), or Van Tieghem (1891). These workers regard the vascular system of the seedling plant as a single unit which is morphologically equivalent in all its parts. The observations in this study seem rather to uphold the work of Dangeard (1889, 1913) in which he indicates that the seedling system is initially discontinuous. He considers that this system consists of a

ings, this is not necessarily always the case. However, spiral and annular elements usually differentiate in tissues which are undergoing elongation, and scalariform and pitted elements in tissues which have ceased such growth (as recently indicated by the work of Smith and Kersten, 1942).

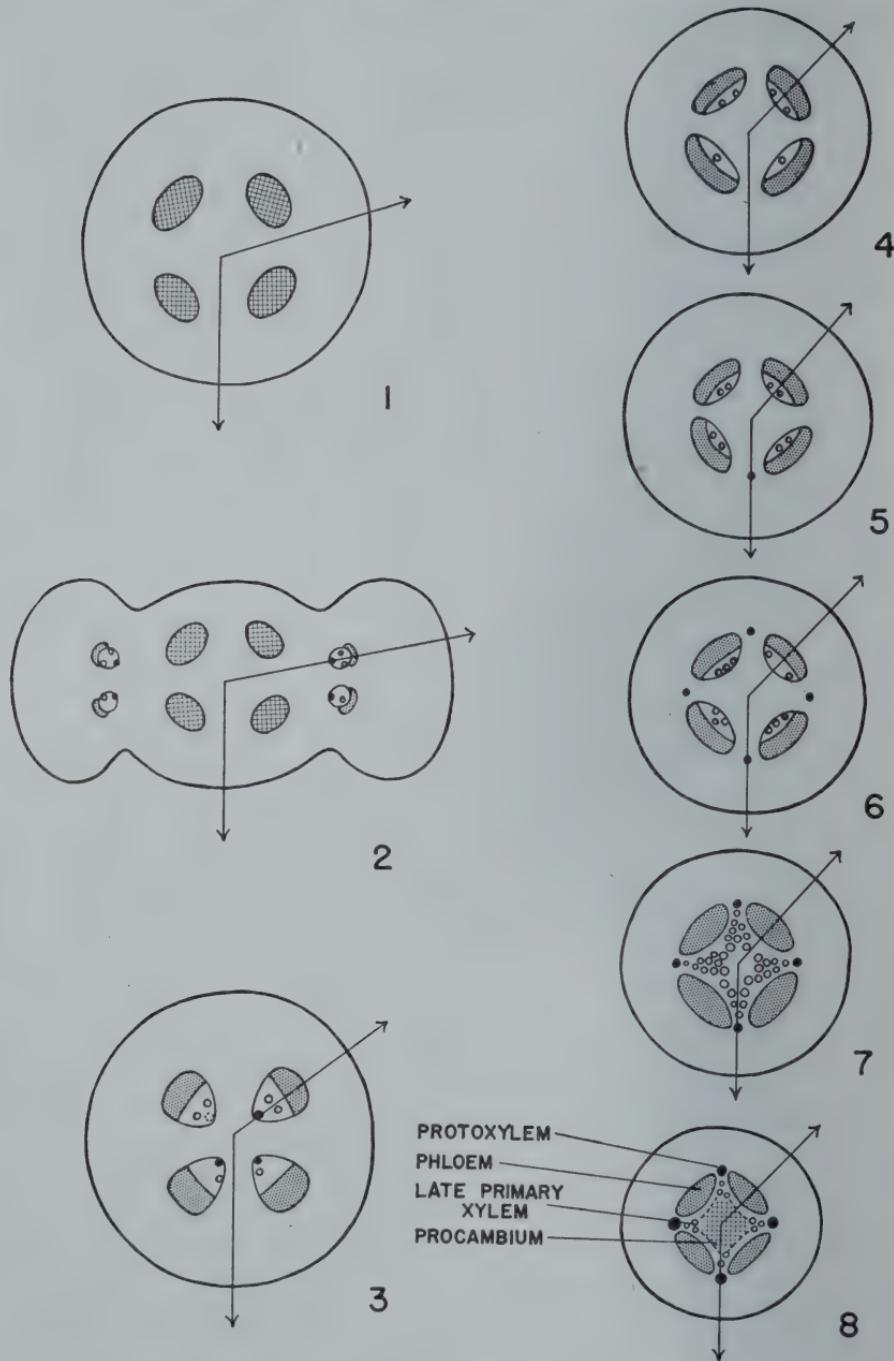


FIGURE 2

SERIES OF SECTIONS THROUGH THE TRANSITION REGION OF A SEEDLING OF *Clerodendron trichotomum*. The arrows indicate the direction of the diagram in figure 3.

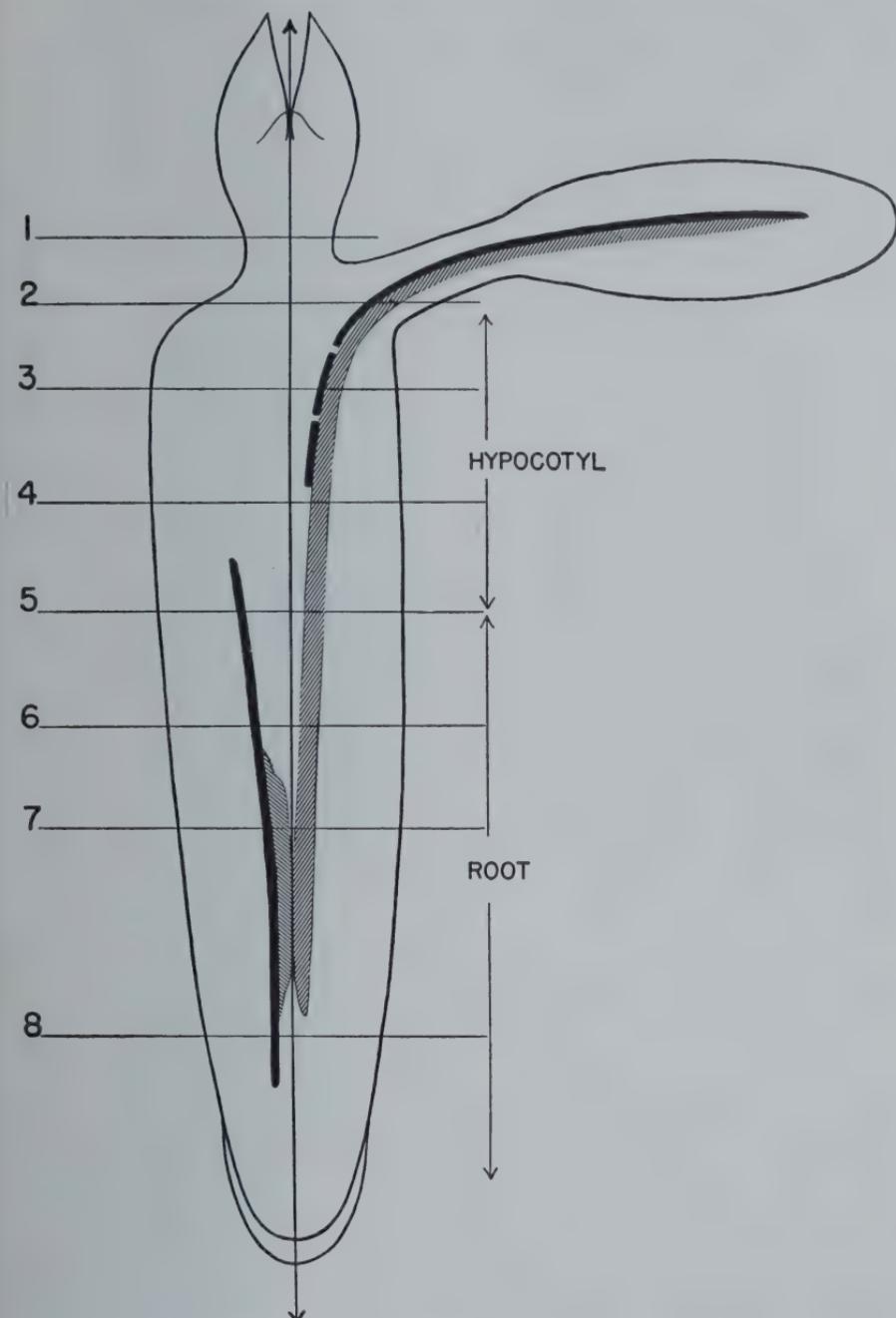


FIGURE 3

LONGITUDINAL SECTION OF THE SEEDLING OF *C. trichotomum* (DIAGRAMMATIC) SHOWING THE POSITION OF THE SECTIONS IN FIGURE 2. First xylem elements are shown in black, later formed xylem is striped. The direction of the diagram is shown on the transverse sections in figure 2.

dicular hypocotylary part and a cotyledonary part and that these two are joined in the upper hypocotyl. This condition would appear to be comparable with the vascular ontogeny observed in *C. trichotomum*. Chauveaud (1911, 1921) also records discontinuity of protoxylem in the majority of the seedlings which he investigated. Paxson (unpublished) found discontinuity of protoxylem in seedlings of *Cucurbita texana*. Lehmburg (1923-24) observed no twisting or rotation of xylem and phloem groups in the transition region of seedlings of *Helianthus annuus*, although the arrangement and number of traces in *Helianthus* does not correspond with those observed in this investigation on *Clerodendron* seedlings.

The arrangement observed by Hill and de Fraine (1913) and Thomas (1907, 1914), where a median protoxylem cotyledonary pole forms the protoxylem point in the root, is not comparable with the condition previously described for *C. trichotomum*. At the stage of development of the seedling where the epicotyl has not elongated, there is no differentiation of protoxylem in the shoot but the xylem of the cotyledons and root are more or less continuous. Compton (1912) and Muller (1937) examined certain hypogaeal leguminous seedlings and observed that the transitional characteristics of the vascular system extended quite far up into the epicotyl, sometimes through more than one internode. In *C. trichotomum*, however, vascularization of the transition region is completed before the epicotyl elongates, and although this plant also is hypogaeal, the transition region does not extend above the cotyledonary node.

Thoday's (1939) physiological theory explained the separate centers of differentiation in a seedling. He suggested that the two opposite poles of the axis, viz. of the root and of the shoot, are capable of impressing their own pattern on the meristematic tissues which they produce, and that the leaf primordia and cotyledons influence the structure of the upper part of the seedling axis, as does the root at the base. In *C. trichotomum* where the epicotyl elongates only after the cotyledons, transition region and root are vascularized, it would appear that the pattern is determined principally by (independent) influences arising in the cotyledons and the root.

In only one of about 30 seedlings studied was there any indication of a median annular or spiral xylem element between the double procambial groups of the cotyledons. In this seedling the median protoxylem element was separated from the endarch cotyledonary protoxylem by parenchyma and was not associated even at a later stage with any metaxylem or phloem. The median protoxylem was also stronger below the cotyledonary node, and was connected with the protoxylem strands which alternate with the collateral bundles in the hypocotyl and extend down to form the protoxylem poles of the root. It would therefore seem best to interpret this median "trace" as an upward extension of the protoxylem of the root which ordinarily terminates in the hypocotyl, and not as a true cotyledonary trace. It is possible that such a condition would arise when the root elongates slowly permitting the center of differentiation in the root to impress its pattern at a higher level in the hypocotyl than is ordinarily the case (see Thoday, 1939).

Vascularization of the seedling shoot: Serial sections and cleared specimens of seedlings which possess only one pair of leaf primordia exhibit two distinct procambial strands in each of the young leaves. In the epicotyl the procambium differentiates in four distinct bundles and shortly after these are formed the first phloem starts to differentiate. At the base of each of the leaf primordia a spiral or annular xylem element differentiates in each of the two procambial groups, although this may not occur simultaneously in the four procambial strands. Differentiation of these first-formed xylem elements then proceeds towards the leaf tip, and simultaneously, down the epicotyl towards the cotyledonary node.

By following serial transverse sections through the first pair of leaves and shoot apex, one observes that additional elements, spiral, annular and pitted, may extend approximately 600 micra above the level of the apical meristem (FIG. 4:A). At the base of each leaf primordium there are always two separate groups of elements (FIG. 4:C, D), even though the two may fuse and/or branch higher in the leaf. Above the point of departure of the leaf traces there are only two arcs of procambial tissue in the stem apex (FIG. 4:D). The gaps lie opposite the leaf primordia and each pair of leaf traces passes in through one gap in the stem procambium (FIG. 4:D). The two traces from each leaf join the procambial arcs of the stem, and then approach each other and become connected tangentially by procambium; so that a cylinder of procambium with four endarch strands of protoxylem is formed (FIG. 4:E). Below the node this opens to give four separate procambial strands (FIG. 4:F), down which the protoxylem is progressively differentiating towards the cotyledonary node. It should be pointed out here that the procambial pattern of the shoot appears to be laid down by continuous acropetal differentiation of epicotylary procambial bundles close behind the apical meristem. This is to be contrasted with the strongly discontinuous differentiation of the first-formed xylem described above.

Each procambial group in the epicotyl shows the differentiation of only one or two xylem elements. In cleared specimens it appears that the spiral and annular xylem in most cases is discontinuous, and in this very early stage the pitted xylem can also be discontinuous. As differentiation proceeds the vascular strands become continuous from the leaves through the epicotyl to the cotyledonary node. In all seedlings examined each foliar strand connects with a separate procambial strand of the epicotyl and becomes a separate vascular bundle.

The cotyledonary node in the young condition: In seedlings of the age just described, the differentiation of spiral and annular xylem between the epicotyl and cotyledonary node is not complete and continuous. It is not until the second pair of leaves become vascularized that the xylem of the epicotyl becomes connected with that in the cotyledonary node. No spiral or annular elements differentiate in this region probably since elongation of tissues in the cotyledonary near nodal region is complete, so that only xylem of the pitted type is formed. Moreover, the first scalariform

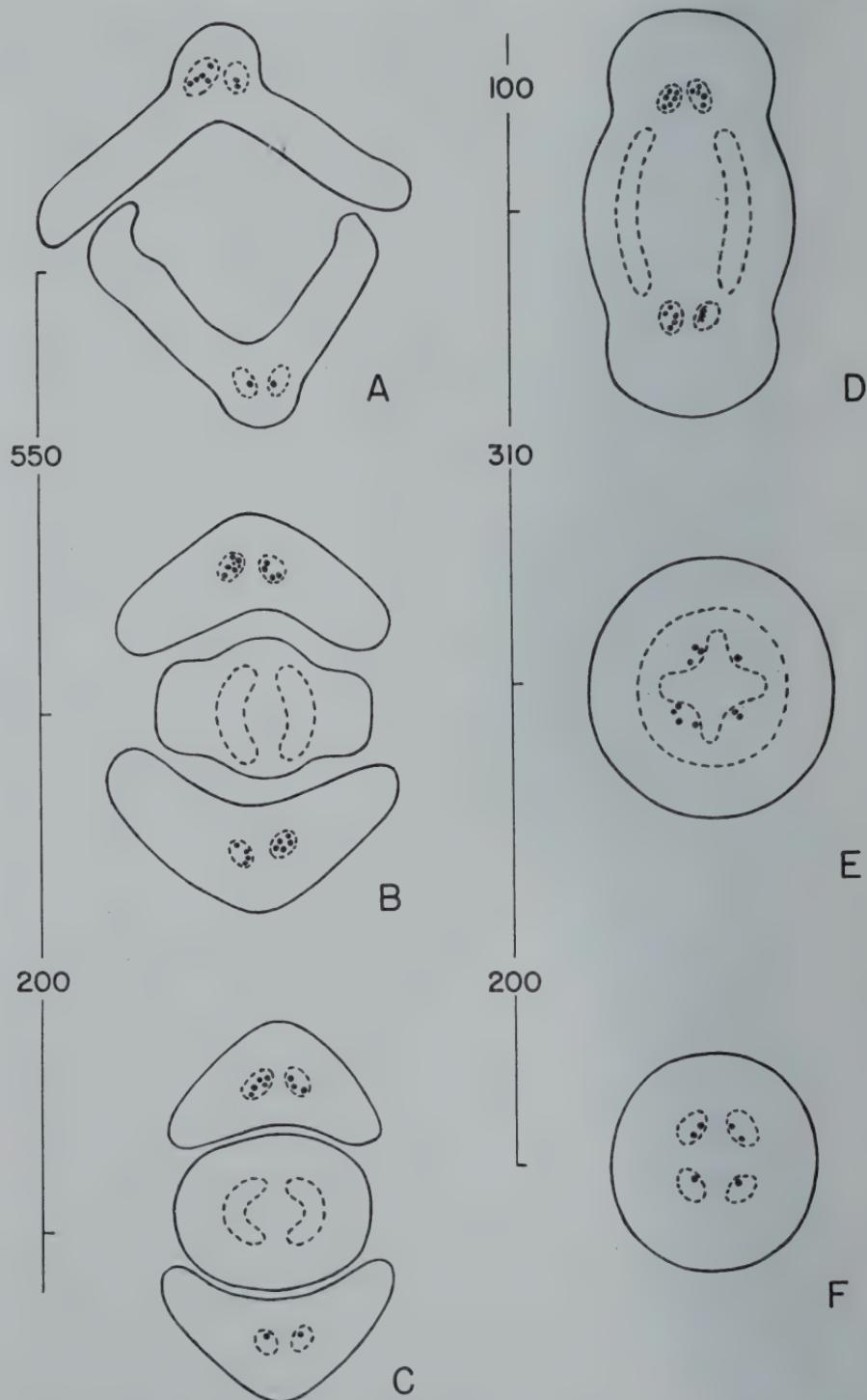


FIGURE 4

A SERIES OF SECTIONS THROUGH THE EPICOTYL OF A YOUNG SEEDLING OF *Clerodendron trichotomum*. Procambium is shown within the dotted lines. First formed xylem elements are represented as black dots. The distance in micra between sections is shown on the left.

xylem to differentiate at the base of the epicotyl becomes continuous with the late-formed primary xylem in the upper portion of the hypocotyl.

Leaf vascularization in older seedlings: In seedlings possessing two pairs of leaves on an epicotyl from 4.5–6 cm. long, the complete vascular connection between the epicotyl and root has occurred. As in the first pair of seedling leaves, the leaves of the second pair each possess two procambial strands. Near the level of the apical mound differentiation of vascular tissue occurs in the second leaf pair in a manner identical with that in the first pair of leaves. A few hundred micra above their bases, these leaves possess several spiral, annular and scalariform elements which may or may not be arranged in two distinct groups. But approximately 200 micra above the leaf base and from here downwards, the differentiating xylem groups are quite distinct. About 200 micra below the apical meristem the leaves attach to the stem and the two strands of each leaf, with 1–4 differentiated xylem elements, join with shoot tip procambium through one gap opposite the leaf base. A small bud procambial trace appears in the axil of each leaf primordium (FIG. 5:D).

At about 120 to 150 micra below the origin of the youngest leaf primordia the leaf trace procambium merges with the epicotyl procambium (FIG. 5:E, F) to form (approximately 100 micra below) a complete cylinder (FIG. 5:G). The protoxylem traces of the youngest pair of leaves now form the protoxylem points of the tip of the epicotyl, and each trace from each bundle of the leaf again forms a separate conducting system which never fuses nor runs together with the other strands for their entire course through the shoot.

Approximately 600 micra below this, the procambial cylinder opens and two procambial bud traces pass out to minute buds in the axil of the first pair of seedling leaves (i.e. the oldest pair of leaves). The shoot at this level now possesses two procambial arcs, each with two xylem groups (consisting of 3 or 4 elements from the youngest pair of leaves) which are continuing to develop acropetally towards the region of maximal area of the second node. 150 to 200 micra below this, the region of maximal area (of the first-formed node) is encountered and at this level two xylem traces of 5–8 elements enter the stele from each leaf base through a unilacunar gap. Now eight distinct xylem groups appear in the procambial cylinder of the shoot and these remain very obvious for about 600 to 800 micra below the region of maximal area of the first node. In cleared specimens the four traces from the youngest pair (second pair) of leaves do not appear to extend much below this point.

Secondary condition superimposed: The picture becomes extremely difficult to interpret in subsequent stages since seedlings possessing more than two pairs of leaves show initiation of cambial activity. Seedlings with only two pairs of leaves have been examined in which cambial activity has already occurred.

The eight xylem groups appearing in the procambial cylinder as described above eventually link with each other at the base of the epicotyl to form four strands just above the cotyledonary node. They do, how-

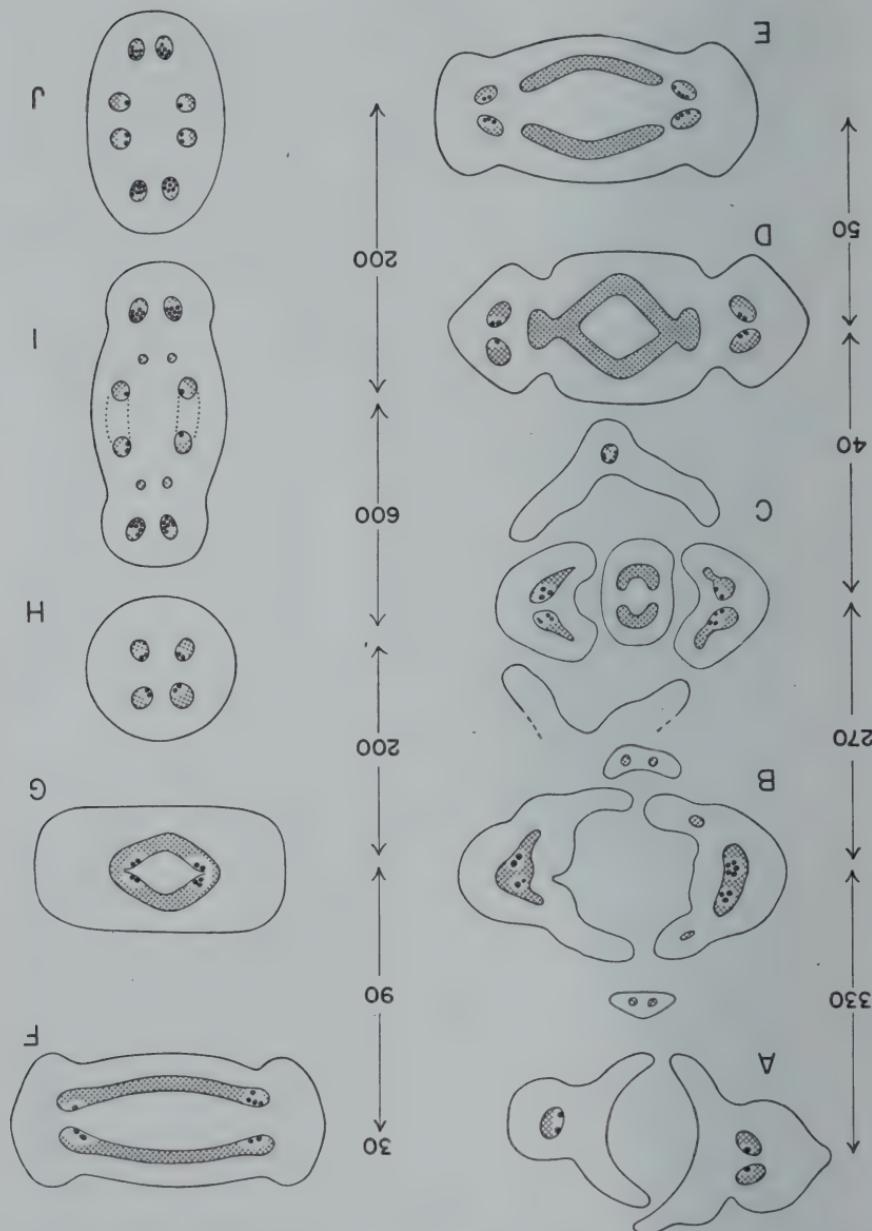


FIGURE 5

SERIES OF SECTIONS THROUGH THE SEEDLING SHOOT TIP WITH TWO PAIRS OF LEAF PRIMORDIA. (*C. trichotomum*). The procambium is shown cross-hatched. First xylem elements are represented in black. The distance in micra between sections is shown on the left.

ever, become connected as a result of secondary activity at a higher level in the epicotyl when a xylem cylinder is formed.

Vascular connection at the cotyledonary node: Careful study of cleared seedlings has shown that the acropetally differentiating pitted elements at the base of the epicotyl become continuous with the cotyledonary traces just below the point of attachment of the cotyledons. The differentiation of spiral and annular elements ceases about 1000 to 1500 micra above this region. However, the pitted elements continue in their acropetal differentiation and two or three parallel elements are apparent in each of the four stem strands. Towards the cotyledonary node the number of pitted elements is reduced so that only one or two elements of each strand become continuous with the pitted elements of the cotyledonary traces. The epicotylary traces join the cotyledonary traces on the inside. In many cases this junction with the cotyledonary traces may be coincident with the differentiation of further strands of pitted xylem centripetally in the lower hypocotyl to form the typical exarch root which possesses a solid core of pitted xylem.

Summary: The important points arising from this ontogenetic study of the seedlings of *C. trichotomum*, which should be emphasized at present, are as follows:

1. In the case of the cotyledons and the first and second pairs of seedling leaves there are two distinct procambial strands which differentiate two annular or spiral elements, and later, at least in the lower one third of these leaves, two xylem bundles.
2. In all these leaf types the two leaf strands are associated with a unilacunar gap in the stele in both the earlier and later stages of differentiation.
3. Each of the two traces from each of the pairs of leaves examined becomes associated with an entirely separate and independent portion of the procambium and later of the vascular eustele.
4. In all cases examined the first-formed xylem of the leaf primordia, the epicotyl, cotyledons and root are discontinuous and therefore neither the protoxylem differentiating from the cotyledons nor that differentiating from the shoot are connected to, or become, the four protoxylem points of the root.
5. The transition region observed in *C. trichotomum* does not correspond with any of the transition types recorded by Van Tieghem or Sargant (1900).
6. A median protoxylem strand does not usually occur in the cotyledons. When one is present it is (1) separate from the two cotyledonary traces and their endarch protoxylem, (2) not associated with any metaxylem or phloem, and (3) stronger below and connected with the protoxylem strands which alternate with collateral bundles in the hypocotyl and extend down to form the protoxylem poles of the root. Therefore it is best interpreted as an upward extension of the protoxylem of the root, which ordinarily terminates in the hypocotyl, and is not a true cotyledonary trace. The

latter is truly double in nature and imposes on the hypocotyl its characteristic fourfold eustelic symmetry.

Further consideration of *C. trichotomum* in comparison with other types of seedlings will be included in the discussion.

NODAL ANATOMY AND VASCULATURE OF LEAVES

Nature and arrangement of foliar buds: As in plants of *Syringa*, *Betula* and *Euptelea* (Garrison, 1949a, 1949b), the buds of *Clerodendron trichotomum* are of two generations; these have been designated by Garrison as "primary" and "secondary" buds for the plants mentioned above, and the same terminology has been adopted here. The term "primary" is applied to the mature buds which bear embryonic "secondary" buds in the axils of their leaf primordia.

An examination of the primary terminal and axillary buds of the young shoot of adult plants of *C. trichotomum*, shoots of two-year-old plants (with the juvenile habit), and primary buds of seedlings 4 to 6 months old, has been made. The general arrangement of buds in all these stages of development is essentially the same. In *Clerodendron trichotomum* both the terminal and axillary buds are arranged in complex groups (PLATE I:1, 2). In the axil of each leaf there is one main axillary bud, one pair of lateral accessory buds, and usually a single accessory bud below the main axillary bud (PLATE I:1, 2). Additional pairs of lateral accessory buds may be present.

Terminal and axillary buds were collected at various times during the year. In their winter condition, the terminal buds are small, dull red and extremely hairy. Between the middle of April and the beginning of May, the buds open and the new year's growth is formed. At this time many of the axillary buds grow into lateral branches also (PLATE I:1, 2). Winter buds usually consist of one or two pairs of cataphylls, and two or three pairs of leaf primordia. In the spring condition the number of leaf primordia increases giving between 6 and 12 pairs of leaf primordia.

In many cases a delay in the opening of the terminal buds has been observed and the axillary buds at the first node elongate rapidly at the beginning of the new season producing the much branched condition of the adult plants. Shortly after the new growth of terminal and axillary buds, the cataphylls (PLATE I:1) drop off (PLATE I:2); the first two foliage leaves (the transitional leaves), which are much reduced in size (PLATE I:2), are also shed after a time. The terminal and lateral branches elongate rapidly producing, in the mature plant, adult leaves (PLATE I:1, 2) and in the seedling plants (1 to 2 years old) the enlarged juvenile leaves.

Origin, development and vascularization of buds: During the elongation of the terminal buds, and of those axillary buds destined to become lateral branches, the leaf primordia mature into leaves. The apical meristem of such shoots retains its meristematic properties, producing the leaf primordia of a new primary bud in the late spring and summer. The

apical meristem and the production of leaf primordia and secondary buds is similar in terminal and axillary (primary) buds.

From the time of its initiation, the tissues of the first pair of minute leaf primordia and of the apical mound are all meristematic. As the second pair of leaf primordia are initiated, a small mound of meristematic tissue becomes obvious in the axil of the leaf primordia of the second node. This meristematic mound is delimited from the terminal meristematic tissues in the leaf of whose exil it occurs during the next plastochrone³ by a layer of cells which are cambial-like in appearance; these form what is known as the shell-zone (Schmidt, 1924). Hence the first secondary bud is detached in primary buds in the axil of the third leaf in *Clerodendron trichotomum*. As this secondary bud assumes a position at the fourth node from the apex, it becomes more obvious due to the extensive vacuolation of surrounding cells in the cortical and pith zones. Each bud primordium which is formed in this manner has been termed a "detached meristem" (Wardlaw, 1943).

In these detached meristems during the third to fifth plastochrones of the leaves in whose axils they occur obvious procambial tissue is differentiated continuously and acropetally in connection with that in the axis, before these secondary buds produce leaf primordia. Two strands of procambium differentiate on each side of the secondary bud primordium, giving four procambial strands in all. These bud traces continue to differentiate acropetally into the first pair of leaf primordia which are produced by the secondary bud later in the season; the bud traces thus become the strands of the first pair of cataphylls.

From the time that the apical mound of meristematic tissue of a secondary bud is delimited from the meristematic tissues of the primary bud, to the elongation of the mature bud (now primary) with all of its leaf primordia, 16 or more months elapse. Detached secondary bud meristems become obvious in September or October. Both primary and secondary buds remain dormant until the following February or March, and only then are the first leaf primordia produced by the secondary bud meristem. One or two pairs of cataphylls, one pair of transitional leaves, and one or two pairs of foliage leaves are produced between March and April of this year. In March, the production of these bud primordia is preceded by marked enlargement of the bud primordia due to rapid cell division. The first pair of leaf primordia of the secondary bud develop at right angles to the subtending leaf primordium of the primary bud. Subsequent pairs of leaf primordia are initiated in an opposite and decussate arrangement. The first two or three leaf primordia thus produced become cataphylls. By the time the primary buds open and the axis starts to elongate the cataphylls and the first pairs of leaf primordia of the secondary buds

³ Askenasy (1880) used this term to denote the interval of time between the appearance of two successive leaf primordia on the shoot apex. It has been used here also for successive intervals of time in the development of any one leaf primordium, viz. a leaf primordium may be 2, 3, 4, etc. plastochrones old. The interval of time for the formation of a leaf primordium is its first plastochrone.

have been produced. By September the remaining pairs of leaf primordia have been produced. These buds, now "primary," elongate the following spring.

The sequence of events in the development of primary and secondary buds of *Clerodendron trichotomum* described above is essentially the same as that observed by Garrison (1949a, 1949b) for *Syringa*, *Betula*, and *Euptelea*.

Vascularization of buds: Esau (1943b) has pointed out the lack of information on the development and vascularization of axillary buds, and the need for more complete investigations of this kind. She emphasizes (1953) the importance of considering vascular differentiation in both transverse and longitudinal directions, since these occur simultaneously. This investigation has been primarily concerned with the differentiation of xylem in connection with the foliar and nodal anatomy, but as far as it has been possible, procambial and phloic differentiation have also been considered. The following description of differentiation applies to both terminal and axillary buds unless otherwise stated.

Longitudinal course of differentiation: PROCAMBIIUM.—Procambial tissue is not easily distinguished from the cells of the meristematic region and its course can only be followed with difficulty. Frequently procambium is not observed when sections are cut obliquely, or when the procambial strands themselves run obliquely at the nodes due to leaf gaps. In this study procambial tissue has been recognized by (1) its ability to stain more densely than the surrounding tissues, and (2) its narrower cells, which are elongated parallel to the long axis of the bud (cf. Esau, 1942, 1943b and 1953).

The differentiation of procambium during bud formation in *Clerodendron trichotomum* is continuous and acropetal in both primary and secondary buds. The procambium differentiates in connection with the previously existing procambium of the axis, acropetally into the leaf primordia and also into the secondary bud primordia (before they produce leaf primordia). The meristematic tissue of the apical mound and the first pair of leaf primordia is in continuity. When the production of leaf primordia is rapid, procambium does not differentiate into a pair of leaf primordia until the next plastochrone, when secondary buds are initiated in their axils. If, however, leaf primordia are initiated more slowly (at the beginning of leaf production in March and April), then procambium differentiates acropetally into the first leaf primordia during the second plastochrone. This acropetal differentiation of procambium is in accordance with procambial development in *Phlox* (Miller and Wetmore, 1946), *Linum* (Esau, 1942), *Syringa*, *Betula* and *Euptelea* (Garrison, 1949a and b).

In *Clerodendron trichotomum*, two distinct procambial strands (FIG. 6:B) differentiate into each leaf primordium during the third to fifth plastochrone after its formation. Four separate procambial strands differentiate into each secondary bud primordium (FIG. 6:B). Precocious procambial production such as described for *Linum perenne* by Esau (1942) has not been observed in *C. trichotomum*. No difference has been observed

in the differentiation of procambium to cataphylls, transitional leaves and foliage leaves.

FIRST-FORMED PHLOEM.—As in the seedling, the phloem is the first vascular tissue to differentiate in the vegetative buds of the mature plants of *Clerodendron trichotomum*. The first-formed phloem differentiates continuously and acropetally, following the pattern mapped out for it by the procambium. The first-formed phloem elements have been recognized in this study by their early vacuolation, loss of nuclei, thickening of the cell wall (nacré appearance) and the formation of sieve plates. Differentiation of the first-formed phloem may occur in the bases of the first leaf primordia, if production of leaf primordia is slow. During the third plastochrone of this leaf primordium, differentiation of phloem is completed (FIG. 7:B). If the production of leaf primordia is more rapid the first phloem elements can be recognized in the second pair of leaf primordia.

Two separate strands of first-formed phloem differentiate acropetally into the base of each leaf primordium, one on the abaxial surface of each procambial strand. Similarly, four strands differentiate into each secondary bud primordium, about the time that the first pair of leaf primordia are produced in that bud. The first-formed phloem elements differentiate to the base of each of the first pair of leaves, so providing the bud primordium with a vascular connection to the main axis.

FIRST-FORMED XYLEM.—The first-formed xylem elements differentiate considerably later than the first-formed phloem elements. The timing of their differentiation is extremely variable and is connected with the rate at which leaf primordia are produced. If production of leaf primordia is slow, some xylem may be produced in a leaf primordium during its third plastochrone (FIGS. 6:B, 7:B). However, during more rapid production of leaf primordia the first xylem elements may not be differentiated in a leaf primordium until its fourth or fifth plastochrone. In either case, differentiation of the first-formed xylem elements is by-directional and discontinuous. A strand of first-formed xylem appears on the adaxial side of each of the two procambial strands; these xylem elements were recognized by the use of the criteria Esau has cited (1942). They are initiated at the base or some distance above the base in the leaf primordium. In either case differentiation occurs in two directions simultaneously, viz. acropetally towards the tip of the leaf primordium, and basipetally towards the main axis of the bud. The basipetally differentiating first xylem elements meet and join with acropetally differentiating first-formed xylem in the main axis of the bud. The actual union of these traces does not occur until about the fifth plastochrone of the leaf primordium in whose axil the bud occurs (FIGS. 6:B, 7:B).

Differentiation of the first xylem elements in the secondary bud primordia does not occur until the fifth plasochrone of the leaf in whose axil it occurs although mature phloem may be present much earlier. A secondary bud at this time has two or three pairs of leaf primordia, into which the procambium and phloem have already developed acropetally, as described above. The first xylem elements differentiate acropetally into the base of

the secondary bud in continuity with the xylem trace to the subtending leaf primordium of the primary bud. Subsequently, in the secondary bud itself, the first xylem elements to differentiate are observed, as in the primary buds, at or near the base of the third or fourth pair of leaf primordia. Further differentiation is as described for the primary buds.

*Transverse course of differentiation: PROCAMBIA.—*The first procam-

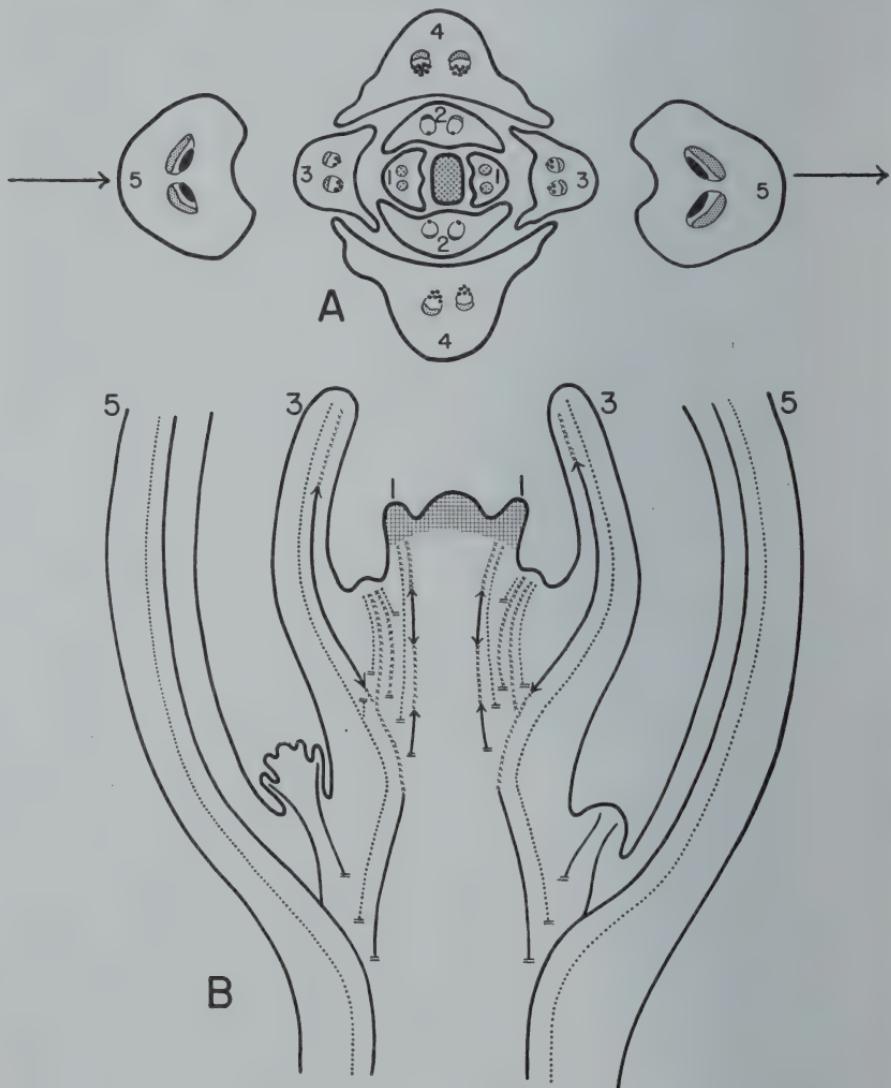


FIGURE 6

THE COURSE OF VASCULAR DIFFERENTIATION IN THE FIRST, THIRD AND FIFTH LEAF PRIMORDIA OF A BUD OF *Clerodendron trichotomum*. Crosses indicate the procambial strands. Phloem is shown as a dotted line. Xylem is represented as a solid black line. The arrows indicate the direction of differentiation. Traces terminating in a pair of transverse lines pass out of the plane of section.

bium differentiates in the main axis below the youngest pair of leaf primordia. In transverse sections it appears as four small groups of densely staining cells, these represent the four procambial traces to the youngest pair of leaves (two strands to each leaf). At this level they appear to be linked laterally by cells with stain-ability intermediate between procambium and ground tissue. These cells constitute what has been termed "less determined meristematic tissue," and will become parenchyma of the interfasc-

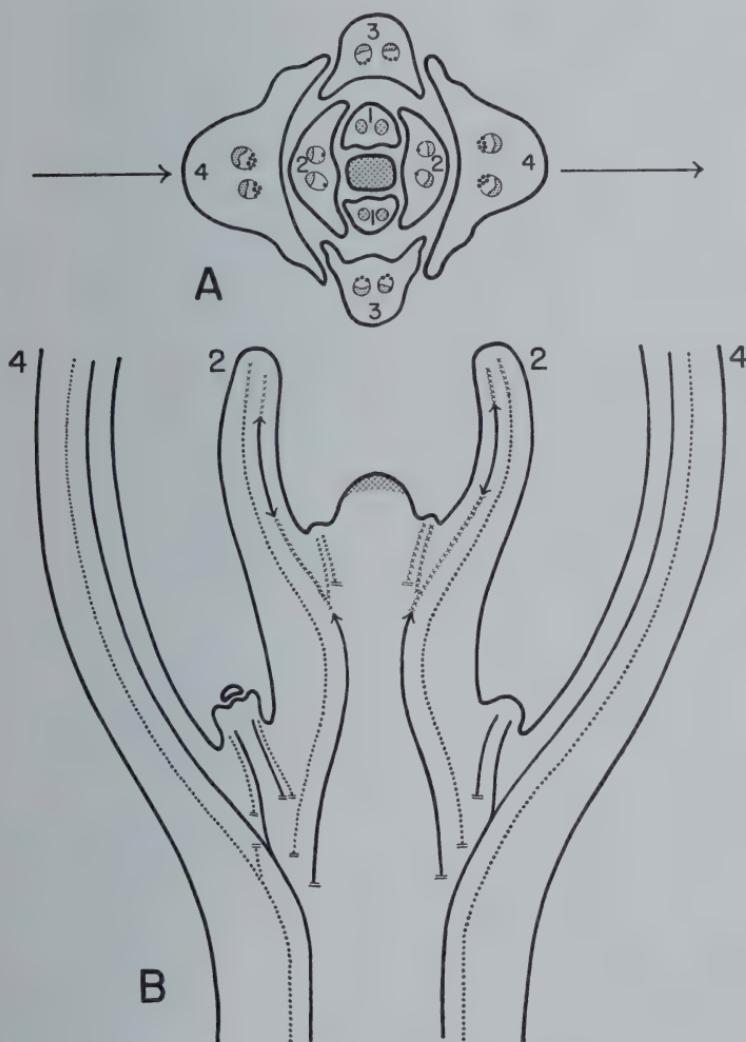


FIGURE 7

THE COURSE OF VASCULAR DIFFERENTIATION IN THE SECOND AND FOURTH LEAF PRIMORDIA OF A BUD OF *Clerodendron trichotomum*. Symbols are the same as in figure 6.

cicular regions and leaf gaps (cf. Esau, 1943b and 1953). The nests of procambium in the main axis divide both anticlinally and periclinally, so building up the four distinct groups in the main axis.

FIRST-FORMED PHLOEM. — The acropetally differentiating first-formed phloem appears in the main axis below the youngest node, and in the second pair of leaf primordia. Its differentiation is initiated on the outside of the axis procambial trace and on the abaxial surface of each of the procambial strands to the leaf primordia (FIG. 6:A, 6:B). Subsequent development of the first-formed phloem is centripetal; laterally it develops in advance of the first-formed xylem elements (FIG. 6:A).

FIRST-FORMED XYLEM. — In the second or third pair of leaf primordia some distance from their point of origin on the main axis, one xylem element differentiates in a median position, on the adaxial surface of each of the two procambial strands. Subsequent differentiation from these first-formed xylem elements is centrifugal in direction. Their lateral spread lags behind that of the first differentiated phloem elements.

The direction of differentiation of procambium, of the first-formed phloem, and of the first-formed xylem elements in *Clerodendron trichotomum* corresponds to that recorded by Esau for *Linum* (1942, 1943a), *Helianthus* and *Sambucus* (1945) (cf. also Esau 1943b and 1954); by Miller and Wetmore for *Phlox* (1946); Garrison for *Syringa* (1949a), *Betula* and *Euptelea* (1949b); and in *Ginkgo* (Gunckel and Wetmore, 1946a and 1946b), *Sequoia* (Sterling, 1945) and *Pseudotsuga* (Sterling, 1947) at least in a transverse direction.

Vascularization of node and internode: Serial sections of primary terminal buds of mature plants, and of four-month-old seedlings have been studied for the initial stages in the vascularization of the main axis. It has not always been possible to follow, in these stages, the course of each foliar strand. For this reason, the nodal structure in the mature two-year-old plant is also described. Thus, as complete a picture as possible of the nodal anatomy of *Clerodendron trichotomum* is given.

Vascularization of nodes and internodes in terminal buds: Serial sections of terminal buds of both adult and seedling plants show identical nodal conditions. For the purpose of simplicity in the following description, bud traces are not considered, but will be discussed in connection with the mature nodal anatomy. The following description is made from the fifth node of a terminal bud upwards towards the apical meristem (FIG. 8). Below the fifth node secondary activity complicates the nodal anatomy.

In the internodal region below the fifth node, six pairs of vascular strands are present. These have been designated as A, B, and C (FIG. 8:1). At a slightly higher level, it appears that the four B strands are double in nature. The A and C strands move apart forming an obvious gap in the eustele as the fifth node is approached, and at this node, the two pairs of A traces pass out to the fifth pair of leaves (from the apical meristem) (FIG. 8:2). At this level also the lens-shaped axillary bud primordia constrict the stele pushing the B and C pairs to the opposite side of the stele, and now four new small strands, D, separate from the two pairs of B

strands. The node, then, at this level, still contains six pairs of vascular strands (FIG. 8:2, 3).

In the internode above the fifth node, the eustele closes and the six

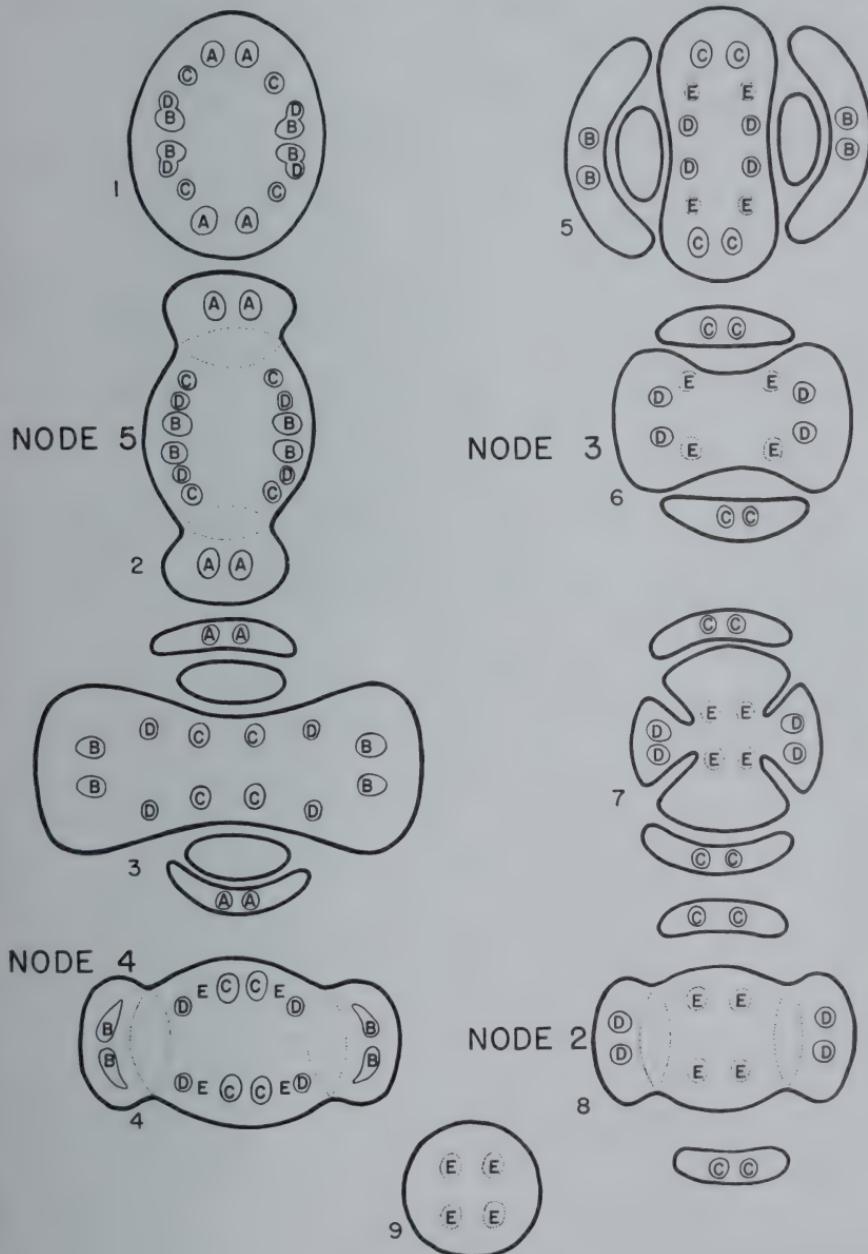


FIGURE 8

A SERIES OF SECTIONS THROUGH THE PRIMARY TERMINAL BUD OF *Clerodendron trichotomum*. Explanation in text.

pairs of strands resume a symmetrical arrangement. The fifth pair of leaves has detached from the axis and each contains two A strands. As the fourth node is approached the B and D pairs separate at either end of the stele, and the two pairs of B traces pass out to the leaves. Again, the axillary bud primordia at the fourth node constrict the stele, and the C and D strand pairs are pushed out of position. Some distance above, where the normal symmetry returns, six pairs of strands are present. The C and D bundle pairs are obvious although there are fewer xylem elements than in the internode below. The four new strands (E) are inconspicuous and procambial (FIG. 8:4). Their origin is uncertain and it may be that at the fourth node they split off obliquely and so were not observed.

From a study of the mature nodal structure, and of the fifth node (cf. above) it is probable that these procambial strands (E) originate from the C traces at the fourth node. However, these procambial strands appear more obvious and stronger in the nodal and internodal regions above. It may be that such a condition could account for the basipetal differentiation of procambium in foliar traces reported by some workers, e.g. Foster, 1935; Kaplan, 1937; Grégoire, 1938; Boke, 1940, etc. However, in the present case the procambial bundle E may run an oblique course and so escape observation where it attaches to the strand C. At higher levels procambium has been observed always to differentiate acropetally into each leaf primordium in continuity with the procambium in the main axis. It has not been possible to observe the course of differentiation of the strand E at its base.

The vascular traces which pass out to the leaves are stronger at the nodes where they depart, than at any other level in the axis. Such a condition would be provided for by the stronger development of procambium strands above the region of their origin.

In the fourth internode there are, then, four distinct pairs of xylem strands (C and D), and two pairs of less distinct procambial strands (E). At the third node the two pairs of leaf traces, C, pass out to the pair of leaves directly above those at the fifth node, and at right angles to the traces passing out at the fourth node (FIG. 8:5, 6). It should be emphasized that the A traces were replaced in position by the C strands, and that the C traces themselves are replaced in position by the procambial strands, E.

At node 2, the two pairs of D traces pass out to the second pair of leaves (FIG. 8:7, 8), i.e. four nodes above their origin from the B strands. Only the four procambial groups (E), now much more conspicuous, remain in the internode above (FIG. 8:9). These pass out at the first node to the youngest pair of leaves.

It appears, then, that opposite pairs of leaves are supplied by separate vascular systems of the stele. That is, the vascular system supplying traces to the pairs of leaves at the fifth, third and first nodes (A, C, and E, respectively) are quite separate from the system supplying leaves at the fourth and second nodes (B and D, respectively). In fact, each leaf in

a separate phyllotactic position is supplied by two quite separate strands in the eustele.

In each case it appears that the traces for any one pair of leaves originate as vascular strands of the eustele at one node, pass upwards through two nodes, and depart to the pair of leaves at the next node above. For example, at the fifth node the D strands arise from the B traces; at the fourth node the B traces pass out; at the second node the D traces pass out.

Vascular structure at the node in adult plants: The nodal and internodal conditions in the adult plant are comparable with those described above, except that secondary tissue has been added. In this condition the vascular strands described above have been identified by their primary xylem groups which project into the pith. At each internode twelve such primary xylem masses can be recognized. Eight of these are always more obvious; these are the strands which will become foliar traces at the next two nodes above. The four smaller primary xylem groups are those which separated, at the node below, from the two pairs of leaf traces which will depart at the node immediately above.

The series of diagrams in figures 9 and 10 illustrates this condition at three successive nodes, A, B and C. Only the primary xylem groups are shown here. At node A, the traces marked 1 depart to the pair of leaves at this node. In near nodal sections the stele separates to form a single gap through which the traces gradually move outwards towards the leaf base; successive pairs of strands become detached from this, and pass into the base of the petiole. Three or four pairs of strands pass out to the leaf from these two separate groups (1) in the axis (FIG. 9). Finally the two traces (1) completely detach themselves from the stele and remain separated from it by parenchyma. At this stage, two bud traces are detached at each side of the axis, from the same traces that supply the leaves, and pass out obliquely to the axillary buds. The vasculature of accessory buds has not been followed in this study. Finally the remainder of strand 1 passes out laterally to vascularize the wings of the petiole as shown in figure 14.

At the same time that the bud traces become detached, two small pairs of primary xylem groups (4) separate from the sides of the larger xylem groups (2) (i.e. in the direction of the departing strands, see FIG. 9) which will depart at the node above (B). In the internode above, the stele again has twelve groups of primary xylem. The four smaller groups (3) (FIG. 9), of the internode below node A, now enlarge considerably and move to close the gap made in the stele by the departing strands (1). Now the eight larger primary xylem groups (3 and 2) are again in opposite positions (FIG. 9).

Similarly, at node B, the four strands, numbered 2, depart through a unilacunar gap in the stele in a similar manner. The number of primary xylem groups is again renewed by the larger traces (3) detaching four small primary groups (5) (FIG. 9). The smaller groups, numbered 4, in-

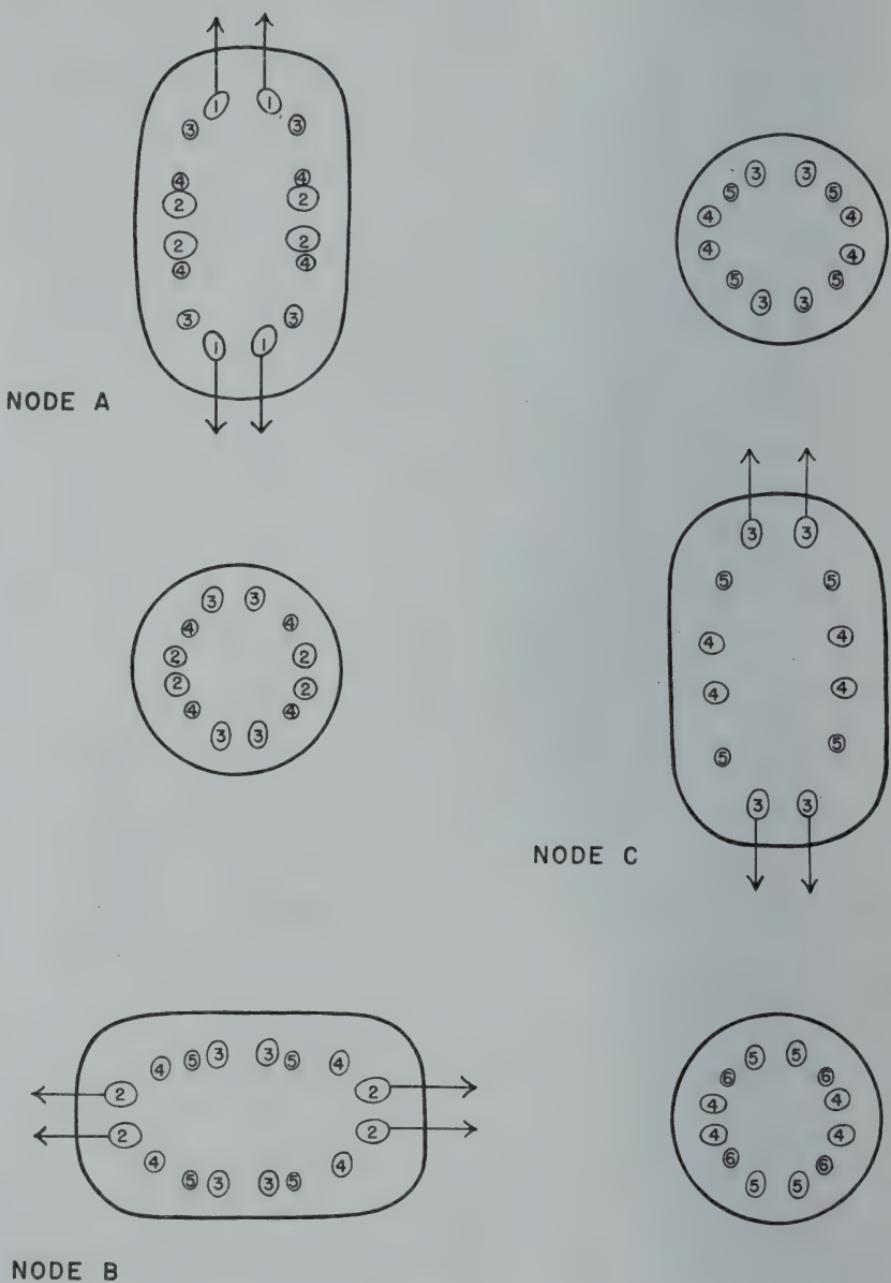


FIGURE 9

DIAGRAMMATIC SERIES THROUGH THE ADULT NODE OF *C. trichotomum*. Explanation in text.

NODE A



NODE C

FIGURE 10

THE LONGITUDINAL COURSE OF THE PRIMARY VASCULAR STRANDS IN THE STEM OF *Clerodendron trichotomum*. Only the vascular strands on the near side of the stem are shown.

crease in size and move into the position of the departing strands to close the unilacunar gap in the internode above B.

The traces, numbered 3, depart at node C and two more groups of primary xylem (6) detach themselves from the enlarged groups (4) (FIG. 9). At the node above C, the traces numbered 4, which originated four nodes below at node A, from traces 2, will depart to the pair of leaves in the same phyllotactic position as those supplied by the traces 2.

In *Clerodendron trichotomum*, where the phyllotaxy is decussate, each leaf is vascularized by two discrete strands that are related to a single gap in the stele. The vascular strands supplying the leaves at alternate nodes arise from independent systems. These systems are only linked laterally by the production of secondary tissue which is not concerned in the foliar supply. The leaves are vascularized from an eight-strand system: the primary vascularization is a system of eight independent strands, consisting of four pairs which independently supply the pairs of traces to leaves in the four phyllotactic positions.

Comparison of Clerodendron trichotomum with other plants possessing a similar nodal anatomy: Several plants possessing a similar unilacunar, double trace condition have been examined. These are described briefly below.

(1) *Ephedra* (By examination of stem tip serial sections supplied by Dr. Taylor A. Steeves, Harvard University) (FIG. 11).

As in *C. trichotomum*, the leaves of *Ephedra* are vascularized by two discrete traces which depart from the eustele through a unilacunar gap. In the slides of *Ephedra* examined, the leaves, as in *C. trichotomum*, possess a decussate phyllotaxy, but, unlike *C. trichotomum*, the scale-like leaves have a sheathing base.

Each internode contains eight bundles in its primary vascular condition (FIG. 11); two pairs of large bundles alternate with two pairs of small ones. At node 1, the two smaller pairs of traces, A, depart through a single gap in the stele (FIG. 11), and the two remaining pairs of bundles (B) branch to form two additional pairs of bundles (C). These two bundles (C) run through one node above (node 2) where these produce two further pairs of bundles (D), and then depart to the pair of leaves at the next node above (node 3). Meanwhile, the two original bundles (now leaf traces B) supply the leaves at node 2 (FIG. 11).

The leaves of *Ephedra* are therefore vascularized at successive nodes from a four-strand system. Each of these four strands supply one of the pair of leaves at every node.

(2) *Austrobaileya scandens* (From examination of serial sections through the terminal bud, first and second nodes of a young shoot. Material from the Harvard University Wood Collection; H-27800, Brass 18160.)

In *Austrobaileya*, as in *C. trichotomum*, the leaves are vascularized by two pairs of strands, through a unilacunar gap in the eustele. Moreover, these arise from two separate procambial strands, although during later stages in differentiation of vascular tissues the strands may appear to

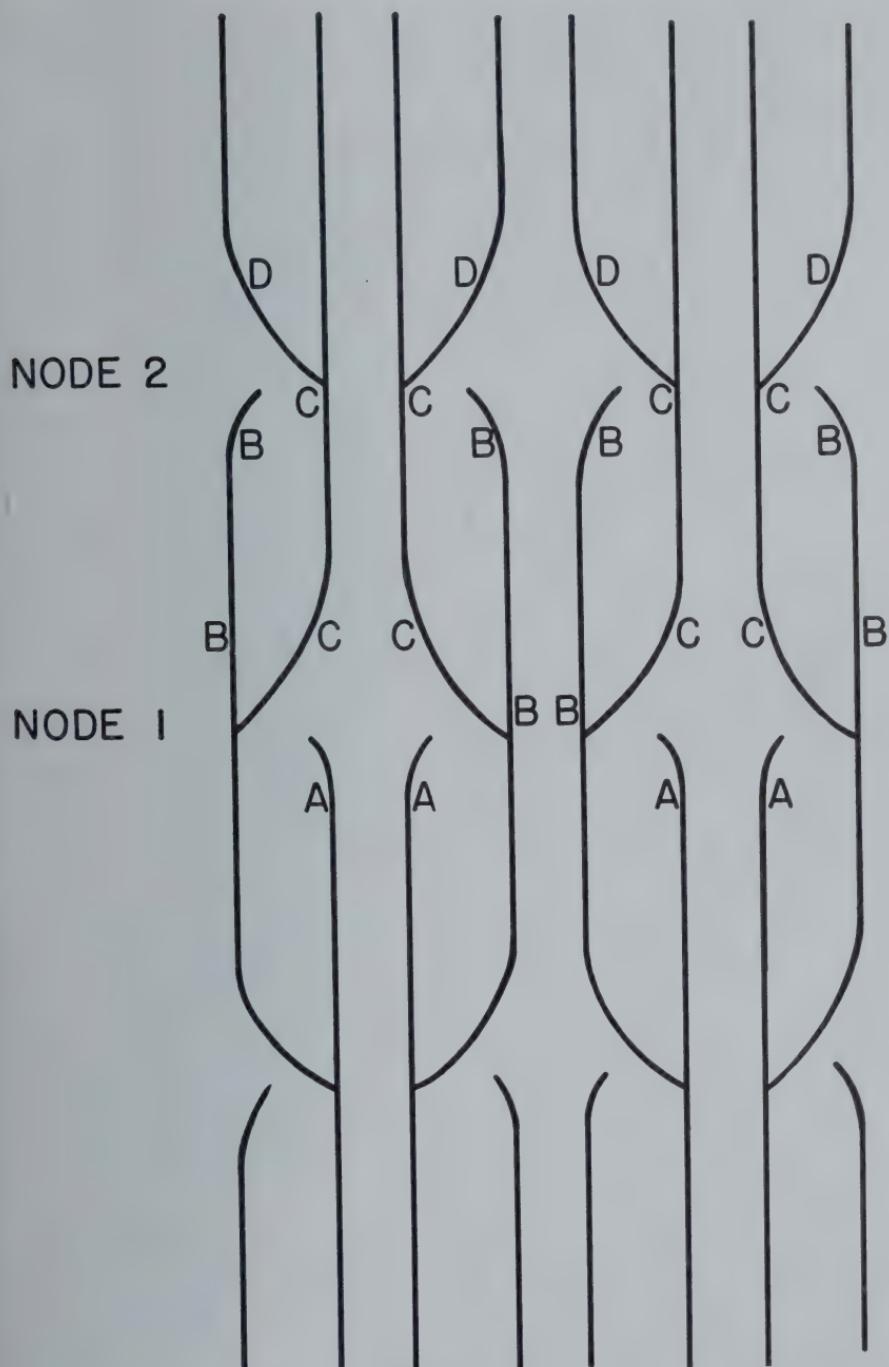


FIGURE 11

THE LONGITUDINAL COURSE OF THE PRIMARY VASCULAR STRANDS IN THE STEM OF *Ephedra*, AS IF SPREAD OUT IN ONE PLANE.

approximate (Bailey and Swamy, 1949). Below the node, the two foliar traces remain independent from one another and arise from two different strands of the eustele. In the young portions of the plant, the phyllotaxy is typically decussate.

As in *Ephedra*, the leaves are vascularized by a four-strand system. This condition is obscured at the first and second nodes by secondary activity. Below the nodes, the four strands supplying the leaves separate into twelve pairs of traces and run with the four-strand system for some distance before passing out to the leaves. However, at each node in the terminal bud, each of the four strands divides to give a trace which will pass out to one of the leaves at the node above (FIG. 12). Therefore, each strand supplies half the vascularization of one leaf at successive nodes, and not, as in *Clerodendron trichotomum*, one leaf only at alternate nodes.

(3) *Trimenia weinmanniaefolia* (From examination of serial sections of the stem through several successive nodes. Material from the Harvard University Wood Collection, H-27965.)

In *Trimenia*, a four-strand vascular system supplies the decussately arranged leaves at each node with four traces (FIG. 13), as in *Austrobaileya* and *Ephedra*. A unilacunar gap is formed in the eustele through which two distinct strands depart to the leaf. However, unlike the condition in *Clerodendron trichotomum*, at each node one of the four strands supplies one of the traces to each leaf (FIG. 13).

A similar condition to that observed in *Ephedra*, *Austrobaileya* and *Trimenia* has been recorded for *Ascarina*, *Hedyosmum* and *Chloranthus* (Swamy, 1953a). *Hedyosmum* and *Chloranthus* show a modification in the division of the foliar traces, however, but possess a four-strand eustelic condition in the stem comparable with that described above for *Ephedra*, *Austrobaileya* and *Trimenia*.

It is evident from the above comparisons that although the leaves of *Austrobaileya* (Bailey and Swamy, 1949), *Trimenia* (Money, Bailey and Swamy, 1950), *Ascarina*, *Hedyosmum* and *Chloranthus* (Swamy and Bailey, 1950; Swamy, 1953a) are vascularized by "two discrete traces arising from two entirely independent parts of the eustele," the strands vascularizing the leaves of *Clerodendron trichotomum* arise from even more independent strands in the stele. In the latter case two quite separate vascular systems are present in the stele, and any one strand supplies the vasculature of leaves in one phyllotactic position only. Four strands supply the leaves at one node, and four entirely separate strands supply the foliar traces at the node above.

Vascularization of vegetative leaves, and comparison with other leaf types: *Adult vegetative leaves — development:* The origin and initial vascularization of leaf primordia has already been discussed in relation to the development of buds. Soon after the production of leaf primordia, and during the third and fourth plastochrones, the marginal and submarginal initials are formed. The subsequent development of these embryonic layers is similar to that described in detail by Esau (1953, pp. 442-447) for ordinary dicotyledonous leaves having an expanded blade,

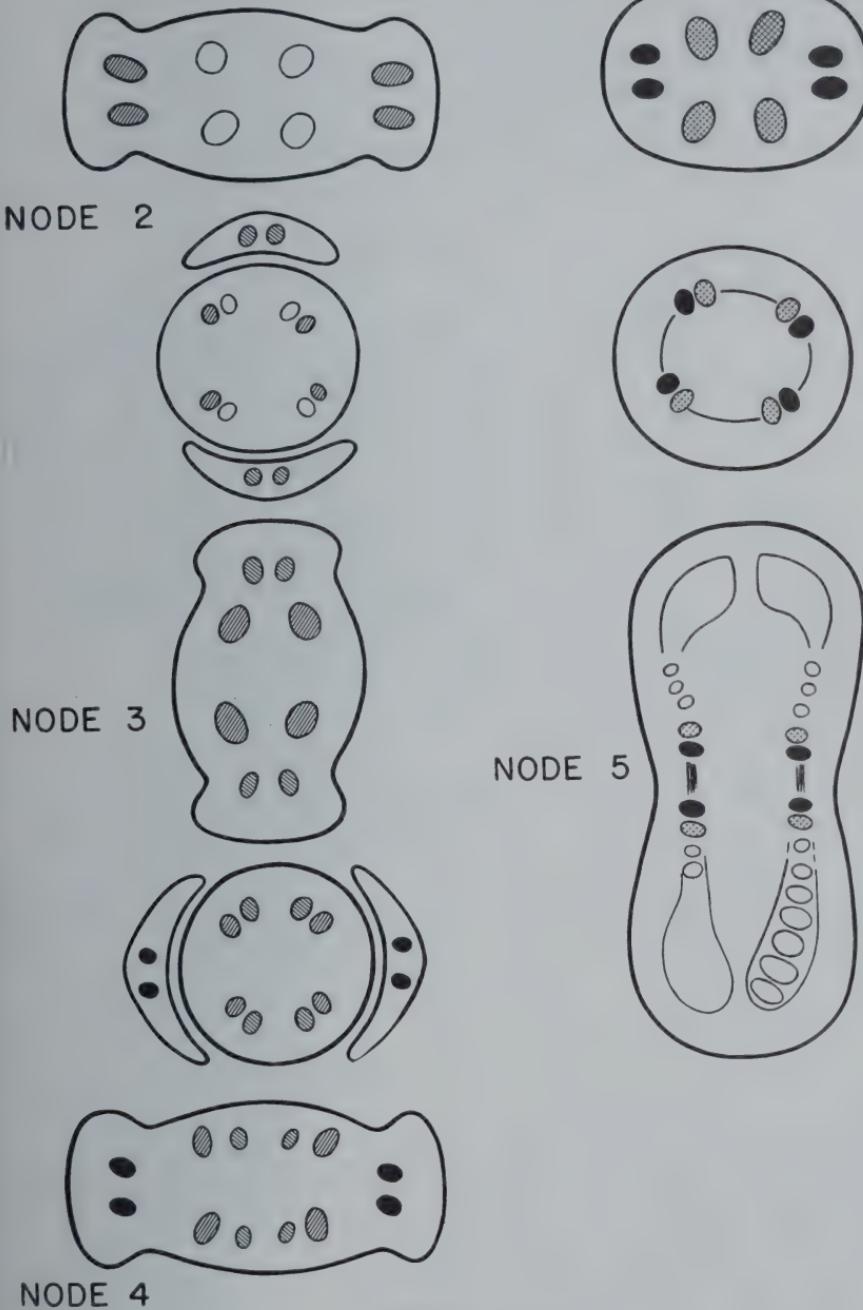


FIGURE 12
THE NODAL ANATOMY OF *Austrobaileya*.

and a petiole, and is comparable with the development of tissues in leaves of *Nicotiana tabacum* (Avery, 1933; Foster, 1936). The details of their development will therefore not be described here.

However, in *Clerodendron trichotomum*, two distinct procambial strands differentiate acropetally into the developing leaf primordia. The vascular pattern is mapped out at an early stage by further procambial differentiation, and each of the two strands is extended to form the procambial

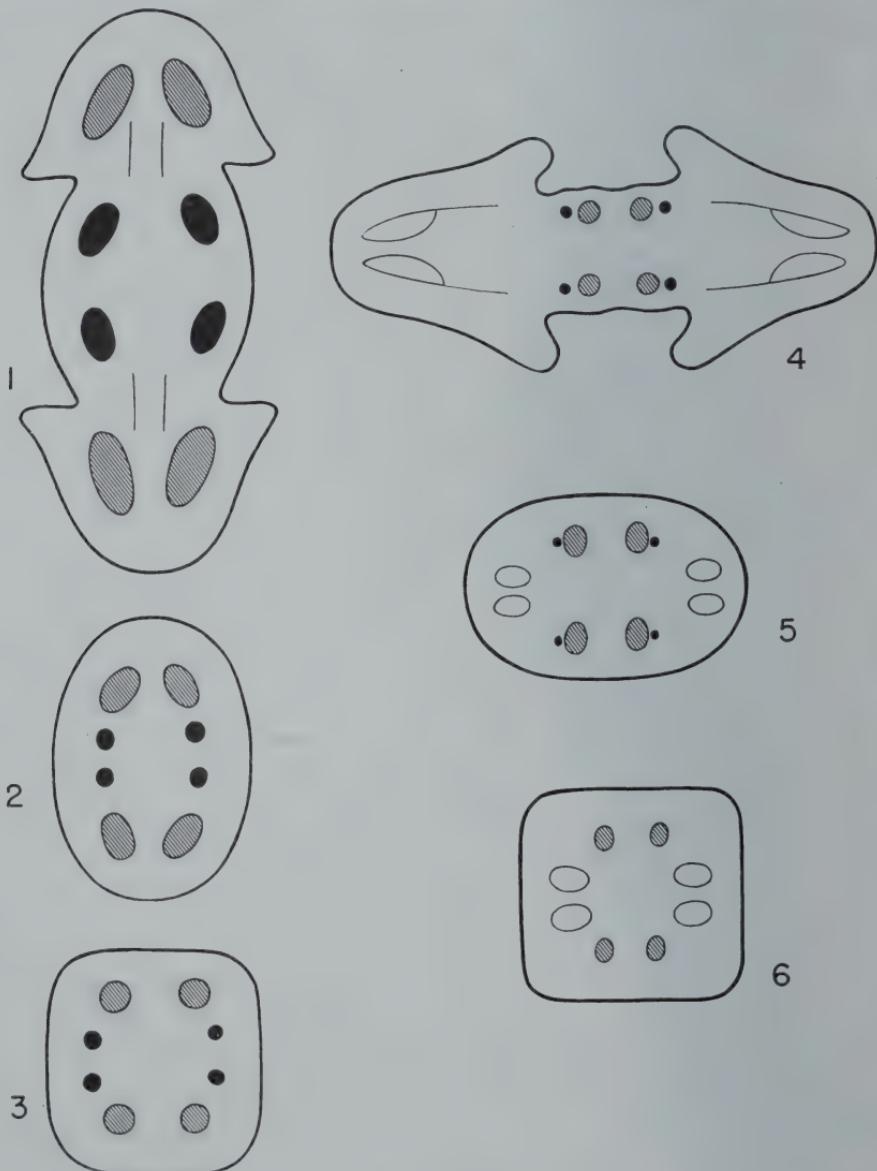


FIGURE 13
THE NODAL ANATOMY OF *Trimenia*.

network of half the leaf. The first vascular tissue to differentiate in the leaves is phloem, and this develops acropetally in continuity with the existing first-formed phloem in the axis. The first phloem is formed in the leaf during its first or second plastochrone. The first xylem elements usually differentiate in a leaf during its fourth or fifth plastochrone. The differentiation of xylem first occurs at the base of the leaf primordium, and is bidirectional and discontinuous. Differentiation of late-formed primary xylem and phloem has not been studied.

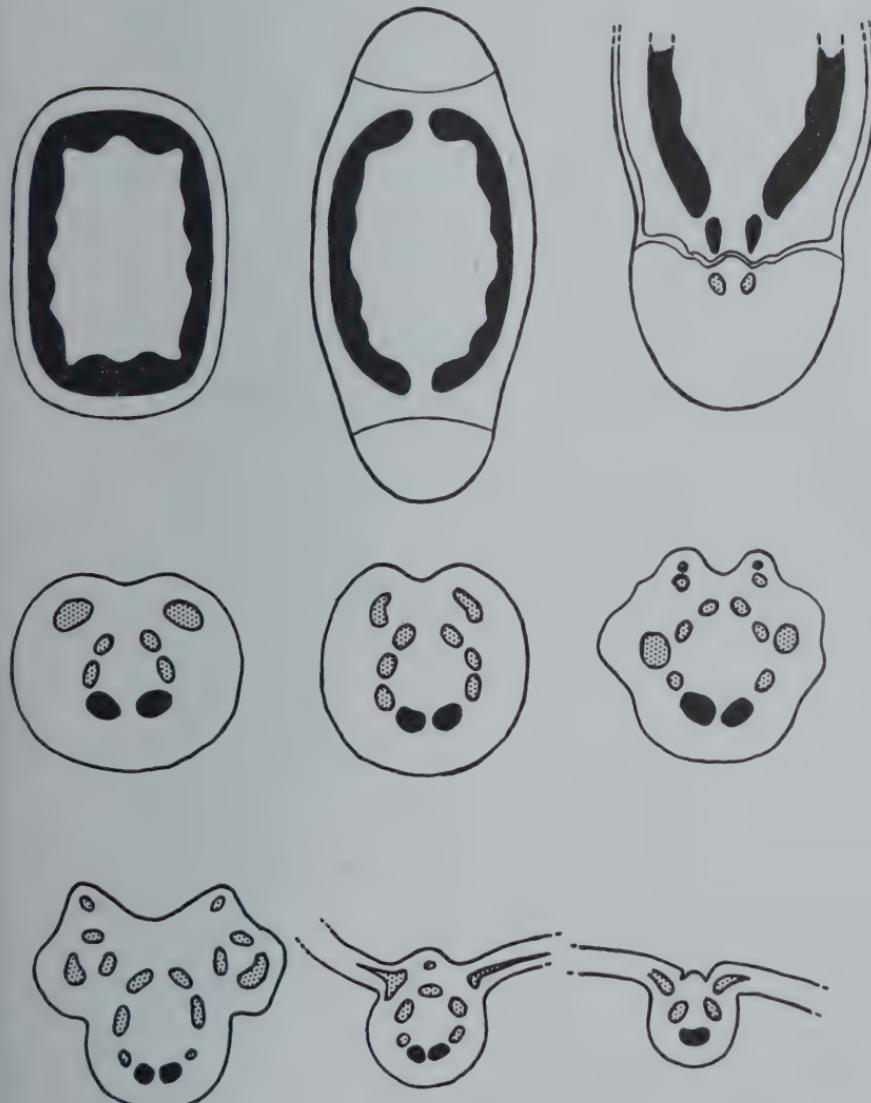


FIGURE 14

A SERIES OF SECTIONS THROUGH THE NODE AND LEAF OF *Clerodendron trichotomum*.

Mature adult leaf — vasculature: In the mature leaf the two leaf traces divide before departing through a unilacunar gap in the stele. The main traces divide to form three or four pairs of subsidiary strands and a pair of bud traces, and finally depart to the base of the petiole. The first two traces to depart to the leaf base form the main strands (shown in black in FIG. 14) of the mid-rib, and these remain distinct throughout the petiole and mid-rib of the lamina, until finally they approximate towards the leaf apex (FIG. 14). The last two strands departing through the single gap in the stele, vascularize the wings of the petiole (FIG. 14). The series of sections shown in figure 14 illustrates the course of the foliar strands through the petiole and mid-rib of the lamina. Throughout the petiole and lower portion of the mid-rib the bilaterally symmetrical arrangement is evident; towards the leaf tip, the number of strands decreases and fusion of the median strands frequently occurs. In many of the cleared specimens examined, the two median strands remained distinct for the entire length of the mid-rib; in some cases, however, fusion occurred towards the tip of the leaf.

Comparison of vasculature of adult and other leaf types: Juvenile leaves: Apart from the much larger size of the juvenile leaves, their vascular pattern is essentially the same as that of the adult leaves. They are also vascularized by two discrete foliar strands, which subdivide as described for the adult leaf form. The two median strands which run through the mid-rib of the leaf may also merge towards the tip of the juvenile leaves.

Floral bracts: The bracts which subtend the trichotomous divisions of the floral axis are vascularized by two strands which arise in a similar manner to those which supply the ordinary vegetative leaves. These strands also depart through a unilacunar gap in the stele. In cleared specimens, the strands remain distinct and each appears to consist of one spiral and two or more scalariform elements (FIG. 15). The bract traces arise from an eight-strand system in a similar manner to that already described for the foliage leaves.

Just below the node where the trichotomy of the floral axis occurs, the two pairs of bract traces become obvious. At about the level where the bract traces separate from the stele, other divisions appear in the vascular cylinder (FIG. 16). These are the regions where the main stele divides to produce three separate vascular cylinders, one for each of the divisions of the trichotomy of the floral axis. The bract strands now depart to the base of the bracts, and these may divide to produce one pair of lateral strands as they do so (FIG. 16). After the two pairs of traces leave the stele, the unilacunar gaps close, forming a horseshoe-shaped vascular cylinder at either end of the elongated axis (FIG. 16) with a third vascular cylinder, medianly placed, which is open at either end (FIG. 16). Constrictions now form in the axis, and all three future floral axis steles become closed. Finally, the stem itself divides into three floral branches (FIG. 16).

In all the cleared specimens of bracts which have been examined, the two median strands remain distinct throughout their length. They do not

appear to merge towards the tip of the bracts, as is sometimes the case in the foliage leaves. The bracts differ from the foliage leaves in their reduced size and narrowly ovate shape. Their vascularization, however, is similar in that they are supplied by two discrete traces through a unilacunar gap in the stele.

Cataphylls: The vascularization of the bud scales has already been discussed earlier in this chapter in connection with leaf primordia. As in the vegetative leaves, and bract scales, the cataphylls are supplied by two separate procambial traces, which arise from the eight-strand system in the same way as the ordinary foliar traces. The subsequent development of the cataphylls is similar to that described by Esau (1953). The vasculature of the cataphylls of *Clerodendron trichotomum* appears, as in the floral bracts, to be limited to the two median strands with occasionally one pair of smaller lateral strands. The cataphylls and floral bracts drop off shortly after the primary vegetative and floral buds elongate.

Transitional leaves: In *C. trichotomum* each bud usually possesses one pair of transitional leaves, just above the cataphylls, which have a more expanded lamina, are green, and lack the great abundance of hairs and cells containing phenolic compounds found in the bud scales. They are, however, reduced in size and transitional in shape between the bud scales and adult foliage leaves. Like the cataphylls and floral bracts, they are shed shortly after the primary buds open. The transitional leaves are supplied with two discrete traces through a single gap in the stele. These traces arise from the eight-strand stelar system in a similar manner to those supplying the foliage leaves and bud scales. However, in the transitional leaves two pairs of laterals are usually produced by the main strands; these latter strands may approximate towards the transitional leaf apex, as in the case of the regular foliage leaves. Hence all these leaf types, the adult and the juvenile foliage leaves, the floral bracts, cataphylls and transitional leaves are similar in their vascularization.

Cotyledons: The vascularization of the cotyledons was discussed earlier. These also are supplied with two discrete strands, although the condition at the cotyledonary node differs from the nodes of the epicotyl. However, the two cotyledonary traces do arise from two separate procambial strands, as is the case in the foliage leaves, cataphylls, transitional leaves and floral bracts.

Considering all the leaf types mentioned above, it is apparent that the vascular supply in all these cases is comparable. Each leaf, regardless of size and form, is vascularized by two discrete strands. In adult and juvenile leaves, in floral bracts, cataphylls and transitional leaves, these two traces arise from the eight-strand stelar system in the same manner, and depart to the leaves, in each case, through a unilacunar gap in the stele. In all six types of foliar appendages the two vascular strands differentiate from two discrete procambial strands in a comparable manner. Hence these leaf types are basically the same and have been modified according to their position and function in relation to the other parts of the plant.

The initiation of an eight-strand vascular system in the seedling: In the

seedling of *Clerodendron trichotomum* there is a four-strand system at the cotyledonary node, which is comparable to the situation observed in adult plants of *Austrobaileya*, *Trimenia* and *Ephedra*. However, in *C. trichotomum*, the cotyledonary traces pass out to the cotyledons directly at their node of origin, and not one node above as in the species mentioned above.

Examination of the epicotyl in seedlings of *Clerodendron* with one pair of leaves only, also demonstrates a four-strand condition. But, between

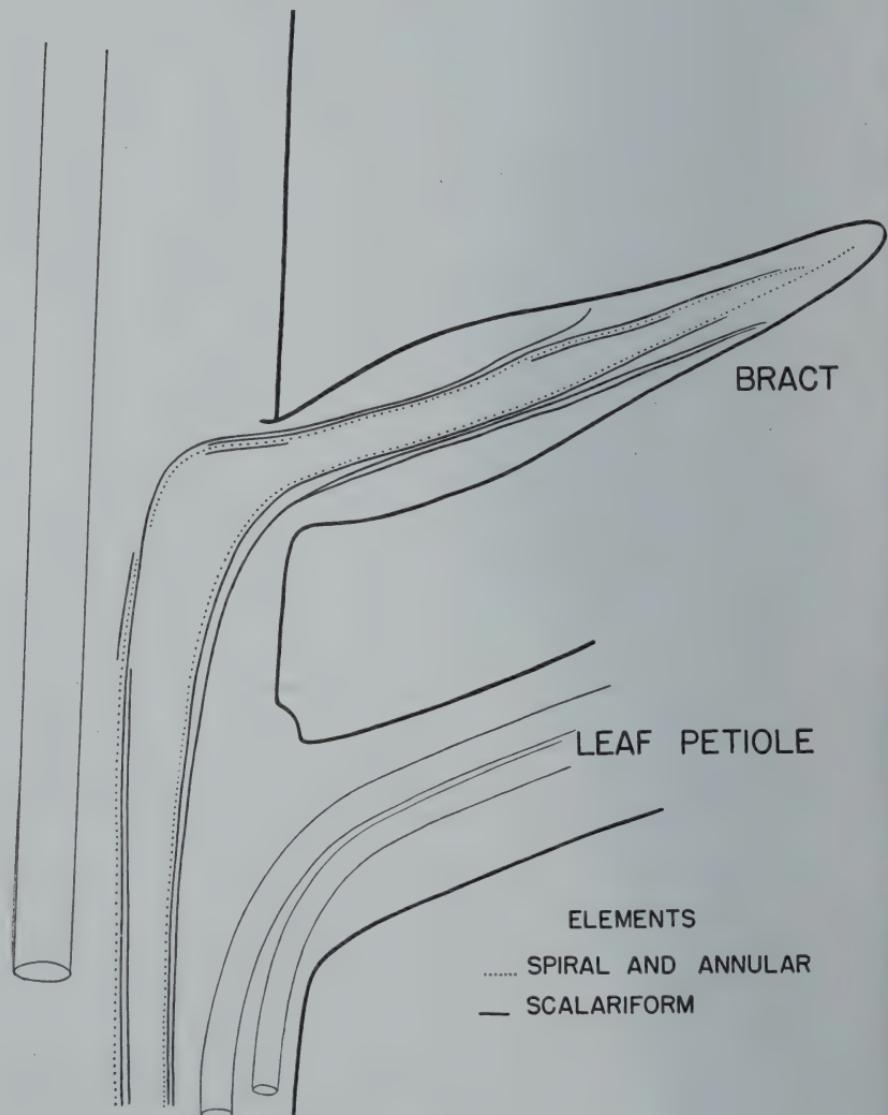


FIGURE 15

DIAGRAM OF A CLEARED FLORAL BRACT SHOWING THE XYLEM ELEMENTS.
(*Clerodendron trichotomum*)

the four first-formed xylem groups of the first pair of leaves, four additional xylem groups differentiate from the next pair of leaf primordia which are produced, so forming the eight-strand system apparent in the adult plant. The xylem of the second group of foliar traces differentiates basipetally down the entire length of the epicotyl to join the late-formed xylem just above the cotyledonary node. There is some variation in the position of attachment of the second group of foliar traces, but in all cases they attach to the late-formed primary xylem between the cotyledonary node, and approximately 1000 micra above. Seedlings with more than two pairs of leaf primordia were not examined and it is therefore not possible to say how the traces to the third pair of leaf primordia arose without further investigation. Foliar traces to subsequent leaf primordia have not been observed in older seedlings in the epicotyl below the first pair of leaf

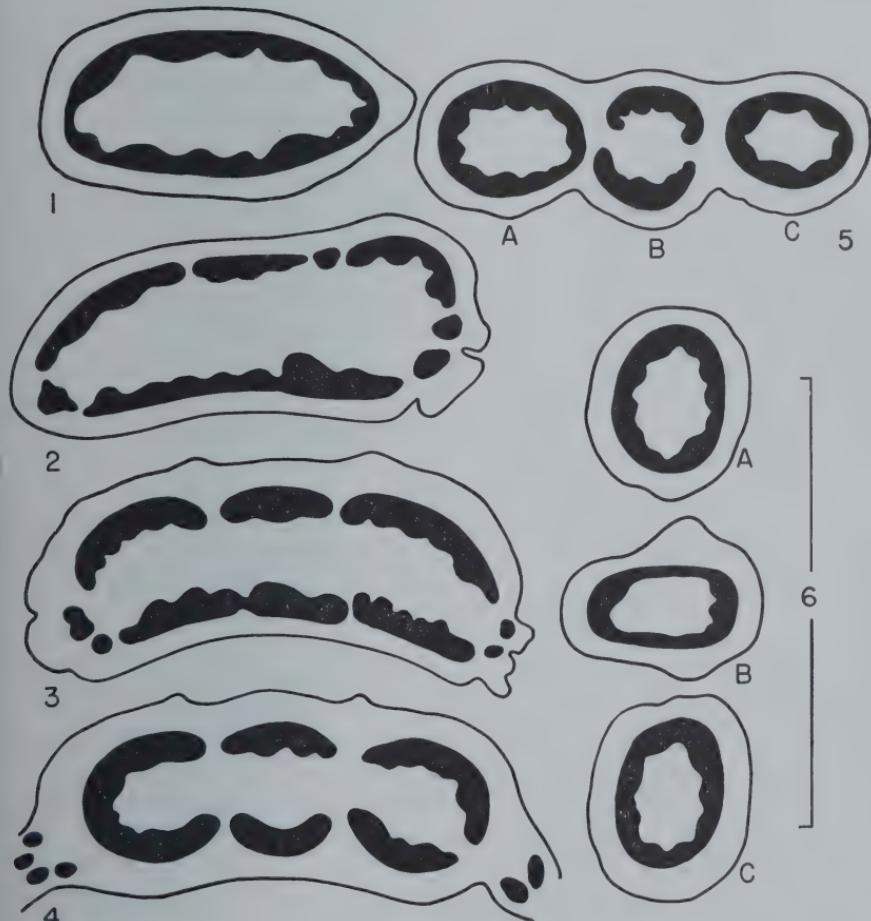


FIGURE 16

A SERIES OF SECTIONS THROUGH THE FLORAL TRICHOTOMY OF *C. trichotomum*, SHOWING THE DEPARTURE OF THE BRACT TRACES.

primordia, and traces to the third pair of leaves may have arisen at the first-formed node from the foliar traces to this pair of leaves.

Summary: (1) In the primary buds: (a) two separate procambial strands differentiate continuously and acropetally into each leaf primordium during the first and second plastochrones. (b) First-formed phloem similarly differentiates acropetally during the second plastochrone. The phloem differentiates first on the abaxial surface of each procambial strand and spreads centripetally. (c) The first-formed xylem differentiates discontinuously (both acropetally and basipetally, simultaneously) during the third and fourth plastochrones, on the adaxial surface of each procambial strand and spreads in a centrifugal direction.

(2) The secondary buds are formed from "detached meristems" during the third plastochrone; differentiation of vascular tissues occurs in a similar manner to that in the primary buds.

(3) An eight-bundle eustelic condition develops in the node; four of these supply foliar traces to the leaves at one node, and four quite separate and independent bundles supply the leaves alternating with these at the node above, i.e. there are two independent systems supplying pairs of leaves at alternate nodes.

(4) Each pair of foliar traces arises at one node, passes upwards through two nodes and departs through a unilacunar gap in the stele to the leaves at the next node above.

(5) All the different types of foliar appendages examined in *Clerodendron trichotomum*, viz. adult leaves, juvenile leaves, cataphylls, transitional leaves, floral bracts (and also cotyledons and the first pair of seedling leaves), are vascularized by two discrete traces which depart through a single gap in the primary stele.

(6) These foliar traces in all cases differentiate from two separate procambial strands, and arise (except to the cotyledons) from two entirely independent bundles of the eight-strand eustele.

(7) The examination of nodal material of *Austrobaileya*, *Trimenia* and *Ephedra* has shown that the leaves in all these plants are vascularized by two discrete traces which arise independently from a four-strand primary stele. The foliar traces in all cases have arisen from two separate procambial strands.

(8) The eight-strand vascular system in adult plants of *Clerodendron trichotomum* has arisen by the basipetal differentiation of the foliar traces of the first two pairs of seedling leaves. Thus, a four-strand, and then an eight-strand system is formed in the epicotyl. There is a four-strand system at the cotyledonary node, since the epicotylary strands become attached to late-formed secondary xylem just above the cotyledonary node.

SUMMARY AND DISCUSSION

Since his survey of the foliar nodal anatomy of dicotyledons (Sinnott, 1914), a fourth type of nodal arrangement, previously known in cotyledonary nodes (Thomas, 1907) but not considered by Sinnott, has recently

been demonstrated to occur at the foliar nodes of a number of dicotyledons (Bailey and Swamy, 1950; Money, Bailey and Swamy, 1949; Swamy, 1953).

The three types of foliar nodal anatomy recognized by Sinnott are as follows:

(a) The *trilacunar* condition, in which three bundles supply the leaf, each causing a gap of its own in the primary vascular cylinder.

(b) The *unilacunar* condition, where one or three leaf traces depart through a single gap in the primary stele.

(c) The *multilacunar* condition where more than three bundles are related to a corresponding number of independent gaps in the primary stele.

Sinnott regarded the trilacunar nodal condition as a very ancient type in the angiosperms, since it occurs in a great majority of the Archichlamydeae. He thought that the unilacunar form was derived from this in some families (1) by the reduction and elimination of the two lateral strands, and in other families (2) by the approximation of the median and lateral strands forming an aggregation of three strands related to a single gap in the stele. The multilacunar form he thought to have arisen by amplification of the number of independently attached lateral strands.

Further, in their series of investigations of the phylogeny of angiosperms, Sinnott and Bailey (1914) regarded the primitive angiosperm leaf as a simple one with palmate venation, possibly stipulate, and provided with three main bundles arising separately at the node. Leaves with parallel venation and those with sheathing leaf bases were observed to be associated with the multilacunar type of node, whereas exstipulate leaves usually exhibited a unilacunar nodal condition. Both of these observations tended to substantiate Sinnott's theory of the derivation of other nodal types by amplification and reduction.

Many dicotyledonous families are predominantly tri-, uni-, or multilacunar but in some families much variation occurs and transitions have been recorded among these three types. The fact that a fourth type of foliar nodal anatomy is now known to occur in the Austrobaileyaceae (Bailey and Swamy, 1949), Monimiaceae (Money, Bailey and Swamy, 1950), and Chloranthaceae (Swamy and Bailey, 1950; Swamy, 1953 a and b), coupled with the common occurrence of such a type of structure in cotyledonary nodes makes it essential to determine whether all types of unilacunar nodes are derived from trilacunar ones since the possibility exists that the fourth type of nodal anatomy may actually be a primitive rather than a reduced one. This fourth type of structure exhibits a single gap through which two discrete strands supply the leaf base, a condition that characterizes many of the gymnosperms and ferns.

The trilacunar arrangement was considered the more primitive condition in the angiosperms since it occurred most frequently in the Ranales and Rosales, which have been regarded as similar to the ancestral angiosperms in other anatomical features. Since the greater number of angio-

sperm families are trilacunar, and since the other nodal forms were thought to be modifications of this by reduction and amplification, its primitiveness has not been questioned until the unilacunar double-trace condition was demonstrated in several ranalian families.

There appears to be insufficient evidence to support the theory that the unilacunar condition is derived in all cases by reduction, especially when nodal arrangements in the vascular plants as a whole are considered. Examination of the transitional forms indicates that the double-trace unilacunar form may be the most primitive arrangement in the angiosperms.

If the unilacunar nodal condition was thought to be derived in some cases by the fusion, or by the loss, of one pair of lateral traces and gaps, could not the single trace of the unilacunar form also have arisen from the fusion of two (unilacunar) traces or by the loss of one trace? In this case, could the primitive number of foliar strands be even rather than odd?

It has been well established that within the woody Ranales primitive morphology of a given plant part is usually accompanied by specialization of other structures, so that no one taxonomic group is conspicuously the most primitive. The primitive characters seem to be divided among a diverse group of families. Therefore, it is not possible to establish which type of nodal anatomy is primitive by correlation with other primitive features; moreover, all four types of nodal anatomy occur in this group. This situation renders dubious Sinnott's correlative argument for the primitiveness of the trilacunar node, and suggests that valid comparative evidence for the primitive nodal condition in angiosperms must consider the Pteropsida as a whole, living and fossil, in an attempt to distinguish the basic nodal pattern in the complex out of which the angiosperms seem to have arisen.

It appears that among the ferns, Cycadofilices, Cordaitales, Bennettiales, Coniferales, Ginkgoales and *Ephedra*, the foliar strand, although often much divided in the petiole and lamina, departs from the primary body of the stele through a single gap. In these groups, the foliar bundles seem often to be *double* in nature.

In most of the Osmundaceae (Tansley, 1907; Scott, 1923; Sinnott, 1911) there is a single foliar strand departing from a single gap in the primary stele. In *Osmunda javanica* Blume (Posthumus, 1924), there is a double leaf trace, each strand with a distinct protoxylem group. The Gleicheniaceae and Ophioglossaceae possess a single gap with one trace, although young stages frequently exhibit a double trace in their first leaves (Bower, 1899, 1908). In all the members of the Marattiaceae, even in young plants of *Angiopteris* though not in the older plants, the condition at the base of the petiole is a leaf trace consisting of *two bundles*, each with a distinct protoxylem group, which depart through a single gap in the stele (Sinnott, 1911). In the fossil ferns of the Carboniferous, *Psaronius* and members of the Botryoptideae, Scott (1900) reports two distinct foliar traces.

Potonié (1896) and Scott (1900) have recorded that most of the Cycadofilices have two distinct foliar traces although fusion of these frequently occurs in the petiole. Sections of the fossil stems of *Lyginodendron Old-*

hamium, *Calamopitys Saturni* and *Medullosa anglica* show two distinct traces passing through the cortex to the base of each petiole, with fusion of these two strands occurring at various levels in the petiole.

The adult plants of the living Cycads exhibit an extremely complex vasculature of the petiole and in some cases the nodal structure is confused by numerous pairs of lateral traces, each of which causes a gap of its own in the stele.

In the Cordaitales, *Mesoxylon* (Traverse, 1950), *Poroxylon* and *Cordaites* (Williamson, 1898) all possessed a double leaf trace departing through a single gap in the stele, which seems to have been typical of the group as a whole. In the Bennettitales, although the vascular supply to the adult leaves is much more simple than in the living and fossil Cycads, the beautifully preserved embryos exhibit the double nature of the vascular strand, and at the cotyledonary node two distinct vascular strands supply each cotyledon, dividing in the tissues of the leaf to form as many as six traces to each embryo leaf (Wieland, 1916). In *Williamsoniella*, however, there is a double trace in adult leaves also (Thomas, 1915).

Jeffrey (1905) indicated the prevalence of a double foliar trace in the Coniferales. In the Abietinae the central strand in the leaf is nearly always double in origin, and this is particularly marked in the early leaves. The two traces are clearly evident in *Araucaria*.

In many of these groups possessing a double foliar strand, for example *Mesoxylon*, *Poroxylon*, *Cordaites*, the Bennettitales and the Coniferales, it has been assumed that these leaf bundles arise from the same main vascular strand (Florin, 1931). These, then, exhibit the continual dichotomy of an initial main strand and uphold the "telome theory" (Zimmerman, 1930). However, in the Ginkgoales and Gnetales, and in several members of the Angiospermae which will be considered later, the two strands of the leaf depart through a single gap in the stele, and each of these is connected to a separate bundle of the eustele.

Ginkgo biloba is reported as having two distinct foliar traces in both long and short shoots (Gunckel and Wetmore, 1946a and b), and Thomas (1907) has observed a similar structure in the cotyledons. The base of the cotyledon is provided with a double bundle and the halves of this separate widely as they pass through the tissues of the embryonic leaves. Gunckel and Wetmore figure the vasculature of the stem and leaf systems emphasizing the connection of each strand of this double bundle with an entirely different and independent bundle of the eustele.

In the seedlings and young adult plants of *Ephedra andina* (Steeves, unpublished) two distinct foliar traces depart from the primary body of the stele through a unilacunar gap (as was also shown earlier in this thesis). These again arise from two entirely independent bundles of the eustele. Sinnott (1914) emphasized that in species of *Ephedra* two distinct gaps occur, but these are gaps in the secondary and not the primary body. This arrangement can therefore be discounted since it is of secondary modification. A similar condition occurs in *Trimenia* and occasionally in *Agathis*. The nodal condition in other members of the Gnetales is ex-

tremely complex in the adult forms, but in the seedlings of *Welwitschia mirabilis* (Rodin, 1953) the cotyledons show two longitudinal vascular bundles entering at the base in cleared seedlings, each dichotomises as it enters the tissue of the leaf and the two lateral bundles of these divide again.

In *Agathis* of the Araucariaceae, a condition similar to that observed in some *Ephedras* has been recorded by Thomson (1913) and the primary arrangement of two distinct vascular strands to the leaves is confused by the insertion of a small segment of secondary wood between the two bundles, causing what appear to be two separate strands in the stele.

This survey of Pteropsida exclusive of the angiosperms can be summarized as follows:

- (1) Almost all of these groups exhibit a unilacunar nodal condition.
- (2) Although frequently there is a single leaf trace, in the majority of the groups examined, two distinct foliar traces depart through the single gap in the primary stele.
- (3) In those cases where a complex condition has been observed in the older plant, the primary condition in the young plants or at the cotyledonary node in the seedling is almost always a double vascular supply to each young leaf or cotyledon from a single gap in the stele.
- (4) Occasionally two gaps occur in the secondary body, but the primary condition in these cases is a single gap with two foliar traces.

This prevalence of the unilacunar, double-trace condition in lower Pteropsida suggests that this nodal arrangement, rather than a trilacunar one, may have been the primitive nodal condition in ancestral angiosperms.

Since the nodal arrangements which occur more frequently in the angiosperms exhibit odd numbers of traces to the leaf base, the question arises as to how these one, three, five, etc. traces could have been derived from the two-trace condition. Since fusion occurs frequently between the two foliar traces of the angiosperms and lower Pteridophyta which possess the fourth type of nodal anatomy, it seems possible that in those cases where a single leaf trace supplies the petiole from a unilacunar gap, this trace may actually represent a fusion bundle.

In *Clerodendron*, *Austrobaileya*, *Trimenia* and *Ascarina* the two foliar traces may unite at varying levels in the petiole or lamina to form a single vein. In *Amborella trichopoda* (Bailey and Swamy, 1948) a single strand appears to depart from a unilacunar gap in the stele, but at sub-nodal levels this strand is seen to consist of two distinct parts which arise from independent portions of the stele (Bailey, unpublished). The fusion of foliar traces observed in the petiole or lamina of the plants cited above has been carried to sub-nodal levels in *Amborella* giving rise to a single trace by the fusion of two initial traces.

Ascarina and *Hedyosmum* of the Chloranthaceae (Bailey and Swamy, 1949; Swamy 1935a,b,c) possess two distinct strands related to a single gap in the stele. In *Hedyosmum* the two strands bifurcate and the two median strands of these then fuse to form a single median strand, while

the two lateral strands bifurcate again, producing a total of five strands. In *Chloranthus* and *Sarcandra*, two vascular strands depart from a unilacunar gap and these immediately bifurcate; the two median members fuse, forming three vascular strands, which become the mid-rib bundles of the leaf. Two smaller subsidiary veins vascularize the marginal portions of the leaf (cf. below).

In the Monimiaceae (Money, Bailey and Swamy, 1950), the family as a whole is uniformly unilacunar. The leaves of *Trimenia* are vascularized by two discrete strands which frequently remain separate throughout the entire petiole and costa of the lamina, each strand supplying by its subdivisions one half of the bilateral leaf, as in *Clerodendron trichotomum*. In some cases, in the leaves of *Trimenia* these two strands may merge to form a single midvein, particularly in the middle and upper portions of the leaf. In all cases the two independent strands arise from two distinctly separate portions of the eustele. In *Piptocalyx* there are two foliar strands which depart from the unilacunar gap, and which bifurcate to produce four strands. The two median strands of this group of four may fuse in the petiole to produce three strands, and in the lamina these coalesce, forming a single midvein. In other words, by a process of bifurcation and fusion, the number of strands has gone from an even number, 2 and 4, to an odd number, first 3 and then 1.

In *Hortonia angustifolia*, *Anthobembix Brassii* and *Mollinedia Rusbyana* (Money, Bailey and Swamy, 1950) (Monimiaceae) increasing odd numbers of foliar traces depart from the unilacunar gap at the node. The number of foliar traces is three in *Hortonia*, five in *Anthobembix* and seven in *Mollinedia*. In each case these arose initially from two distinct strands of the eustele, and this can be demonstrated by following the origin of the foliar traces through several nodes and internodes below.

From the examples cited above, it therefore appears certain that an odd number of foliar traces can arise by the division and fusion of an even number of strands. Particularly, it seems likely that the odd number (1 or 3) of traces related to the median gap of so many angiosperms could have been derived originally from the two-trace condition.

However, the cases of multiple-strand formation mentioned above are not examples of the formation of tri- or multilacunar from unilacunar nodes, because the odd number of strands departs from a single gap as did the primitive pair of traces. Can such multiple traces come to occupy separate gaps? Or is there evidence for the evolutionary addition of lateral traces with new gaps? Acceptance of the hypothesis that the unilacunar node is primitive requires that at least one of these possibilities be demonstrable.

It has been generally accepted since Sinnott's work that the multilacunar condition is specialized, and has been derived from the trilacunar by the addition of laterals with new gaps. It would seem possible for the unilacunar to give rise to the trilacunar in the same fashion. In other words, there is no particular reason to suppose that the kind of amplifica-

tion which resulted in the multilacunar node could not also produce the trilacunar node from the unilacunar one.

The addition of laterals in different gaps to a unilacunar system is adequately shown in the series of nodal forms of Chloranthaceae described by Bailey and Swamy. The primitive form here is undoubtedly the two-trace unilacunar type, as discussed above. However, in *Chloranthus* and *Sarcandra*, where the two traces branch and fuse to form three, as mentioned, two "subsidiary" traces which depart from gaps at right angles to the main gap also vascularize each leaf. The gaps in the eustele in which these traces arise are present but unoccupied in the less specialized Chloranthaceae.

It was mentioned above that in *Agathis* and some species of *Ephedra* a two-trace unilacunar condition becomes converted into an apparent "bi-lacunar" one by development of a wedge of secondary tissue in the gap parenchyma of the stele, between the two traces (Sinnott, 1914). It seems possible that multiple traces in one gap such as were described above for the Chloranthaceae and Monimiaceae could become separated in a similar way and, by extension of this phenomenon precociously to the primary body, come to occupy separate gaps. A tri- or multilacunar condition would thus have evolved.

It is of great interest that a double trace has been recorded in the cotyledons of so many angiosperms (Thomas, 1907) which have an odd number of traces in adult leaves. In the lower Pteropsida also, the double-trace condition is found in the cotyledons in many cases where a more complex and apparently specialized pattern appears at later nodes. On the other hand, among the plants whose mature nodes are unilacunar with two traces, no examples have been found in which the cotyledonary node does not exhibit similar structure (few, however, have been studied). It is tempting to consider that this cotyledonary condition represents the persistence of a primitive morphology. In cotyledons of *Clerodendron trichotomum*, which have been carefully studied with this question in mind, there occurs sporadically a median protoxylem strand which has arisen as an upward extension of a protoxylem pole of the young root and is apparently not a part of the intrinsic vascular pattern of the cotyledons. It seems likely that other cases where three cotyledonary strands have been observed may be instances of a similar complication.

However, seedlings of many dicotyledons (according to an unpublished survey by one of us) have an odd number of cotyledonary traces from a single gap, which are divided from two strands by branching and fusion in a manner similar to that described above for mature nodes of certain Monimiaceae. A common condition (in seedlings) is for the two original traces to branch once and the two median branches to fuse; giving a total of three traces in the petiole. This is found, for example, in Rosaceae, Leguminosae, *Hamamelis* and *Betula*. In others, e.g. *Impatiens* and *Acer*, a greater odd number of strands is produced by further branching. Laterals occupying separate gaps are present in Magnoliaceae and *Degeneria*, though the main gap shows a two-trace condition (Swamy, 1949). The tendency of the unilacunar pair of traces to fuse in the cotyledon, as ob-

served in *Amaranthus* and *Anchusa*, seems to be carried further to form a single unilacunar trace in the Cruciferae, Primulaceae, and *Celastrus scandens*. A pair of distinct parallel traces such as are found in *Clerodendron trichotomum* occurs commonly in Solanaceae and Labiatae.

The median bundle in the uni-, tri- and multilacunar types requires closer investigation. The whole question as to the exact nature of this bundle could be ontogenetic. Does the median bundle represent (a) two distinct procambial strands which have merged during differentiation; (b) two procambial strands, only one of which has differentiated, or (c) only a single procambial strand? And in those cases where there are two distinct foliar strands, are these developed from (a) two distinct procambial strands which have undergone normal differentiation, or (b) the lateral portions of one procambial strand, separated by a median layer which has failed to differentiate into vascular tissue?

In *Clerodendron trichotomum*, all the different leaf forms (excluding the floral appendages) are supplied in a similar manner, viz. by two discrete vascular strands from a single gap. In each case these two foliar traces arise separately from independent bundles of the eustele. In the foliage leaves, bud scales, floral bracts, and cotyledons these two traces originate from two distinct procambial strands. These represent, therefore, two separate procambial strands which have undergone normal differentiation. Similarly, in *Austrobaileya*, where each leaf is supplied by two discrete vascular traces arising from two independent portions of the eustele (Bailey and Swamy, 1949), these foliar traces have differentiated normally from two separate procambial strands. The two separate foliar traces of *Trimenia* (Money et al., 1950) also arise by the normal differentiation of two procambial strands. To the extent that this kind of evidence can indicate the nature of the foliar traces, the present observations suggest that the two leaf traces in the forms studied are distinct, and not the result of abnormal differentiation of a single strand.

This fourth type of nodal anatomy exhibited by *Clerodendron trichotomum*, which occurs in a great many dicotyledonous seedlings at the cotyledonary node, and in the adult plants of several ranalian genera, is a type of nodal structure which must be considered of phylogenetic importance. The double-trace, unilacunar condition does not conform with Sinnott's unilacunar form since it is not attained by modifications of a trilacunar node. The present survey of nodal anatomy, and the ontogenetic studies on *Clerodendron trichotomum* presented here, indicate that the fourth type of nodal structure may ultimately prove to be the nodal arrangement of ancestral angiosperms. In order that such a theory could become a working hypothesis upon which phylogenetic investigations could be based, further extensive ontogenetic studies are needed. It is tentatively suggested here that the unilacunar double-trace condition was the primitive structure of the node among the Tracheophyta, and that the three nodal forms described by Sinnott for the angiosperms are specializations of this. Accordingly, Sinnott's hypothesis of nodal evolution in dicotyledons can be modified as follows (FIG. 17): (a) The two-trace unilacunar condition

can give rise to a single trace by fusion; (b) the double-trace unilacunar condition can give rise to the trilacunar condition by fusion and the addition of one pair of lateral traces and gaps. The trilacunar form can give rise to a unilacunar condition, as it appears frequently to have done, by the loss of laterals, and to a multilacunar form by the addition of pairs of laterals as Sinnott has already postulated.

In conclusion, it should be emphasized that excessive attention has been focused in the past upon the addition or elimination of pairs of independently attached laterals, and to topographical features at the nodal level. Greater consideration should be given in the future to detailed investigations of vascular tissues related to the median gap, and to tracing these structures both downwards in the stem and outwards into the petiole and lamina of the leaf. Bifurcations and fusions of vascular strands, and transitions from an *even* to an *odd* number of such strands, occur at various levels

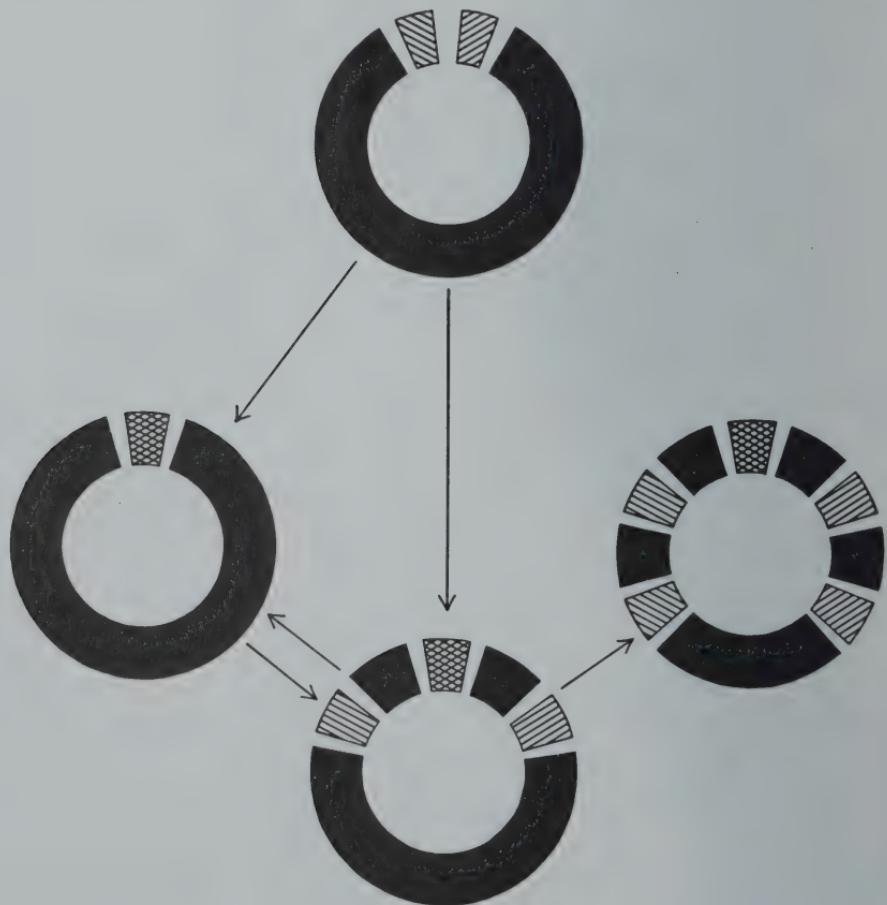


FIGURE 17

THE POSSIBLE DERIVATION OF THE DICOTYLEDONOUS NODAL FORMS FROM THE UNILACUNAR DOUBLE TRACE CONDITION.

of the stem and leaf. Structures which appear to be similar at the nodal level may not be truly homologous, and conversely differences which seem outstanding at the nodal level may acquire a different significance where comprehensive developmental studies at successive levels of the stem and leaf are made.

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PLATE I

1 and 2, expanding terminal and axillary buds of *Clerodendron trichotomum*, showing the cataphylls and transition leaves. Note the retarded growth of the terminal bud (2). $\times 2.5$. 3. Early stages in the germination of the seed of *C. trichotomum*, from left to right of the photograph: (a) Seed with testa removed. (b) Elongation of radicle. (c) Emergence of epicotyl. (d) Beginning of elongation of crook-shaped epicotyl. (e) and (f) Elongation and straightening of epicotyl. $\times 2$.



MARSDEN AND BAILEY, *CLERODENDRON TRICHOTOMUM*

A MONOGRAPH OF THE GENUS PHILADELPHUS *

SHIU-YING HU

Subgenus II. *Euphiladelphus*, subg. nov.Philadelphus subg. II. *Euphiladelphus*, subg. nov.*Philadelphus* Reihe. 1. *Corticatae* Koehne, Deutsche Dendr. 179, 180. 1893.*Philadelphus* Reihe 3. *Decorticatae racemoseae* Koehne, l. c. 180, 182.*Philadelphus* Reihe 4. *Decorticatae pauciflorae* Koehne, l. c. 180, 184, pro parte.*Philadelphus* Sect. 2. *Stenostigma* Koehne in Gartenfl. 45: 450. 1896, pro parte; et in Mitt. Deutsche Dendr. Ges. 1904(13): 77, 81. 1904, pro parte.TYPE SPECIES: *P. coronarius* Linn.

Frutex erectus, inflorescentiis racemosis, vel floribus ternatis vel solitariis, hypanthiis obconicis, subcampanulatis vel subglobosis, glabris vel pubescentibus; staminibus 25 usque ad 90; ovariis semi-inferioribus vel inferioribus; stylis partibus superis plerumque liberis, stigmatibus linearibus vel dilatis; capsulis ellipsoideis vel subglobosis; seminibus longi- vel brevi-caudatis; foliis oppositis, ovatis, serratis, denticulatis vel integris, triplinerviis or quintuplinerviis, gemmis axillaribus inclusis.

This subgenus has a wide range of distribution in the northern temperate zone, between latitudes 25°-50° N. From southern Europe eastward, across the mainland of Asia to Japan and then from western North America to south eastern United States its range is almost continuous. The only two interruptions occur in western and central Asia and the central and northern sections of the Great Plain States in the United States. Obviously the primary cause of these disjunctions is low precipitation. The Amur River region in northeastern Asia and the Columbia River region in western North America register its highest latitudinal distribution and the Himalayan region in Asia and the Rocky Mountain region in North America mark its highest altitudinal distribution. It has 41 species in three sections. Their distributions are as illustrated in Maps 2 and 3.

Section 3 *Pauciflorus* (Koehne), stat. nov.Philadelphus subg. II. *Euphiladelphus* sect. 3. *Pauciflorus* (Koehne), stat. nov.*Philadelphus* Reihe 4. *Decorticatae pauciflorae* Koehne in Deutsche Dendr. 180, 184. 1893, pro parte.

* Continued from volume XXXV, page 333.

Philadelphus sect. *Poecilostigma* Koehne subsect. *Speciosi* Koehne in Gartenfl. 45: 450. 1896; et in Mitt. Deutsche Dendr. Ges. 1904(13): 77, 79. 1904. — Engler, Pflanzenf. ed. 2. 18a: 193. 1930.

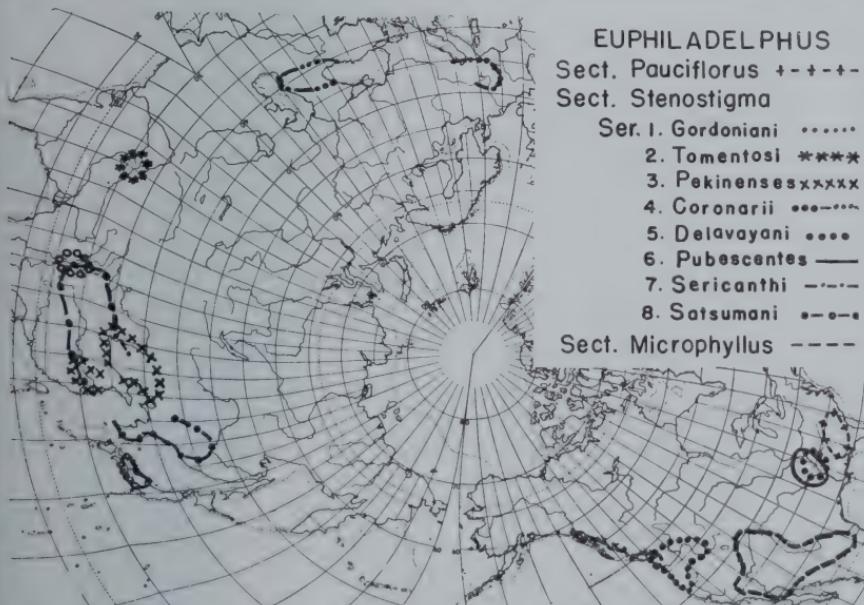
Philadelphus Grandiflori Rydb. in N. Am. Fl. 22: 163. 1905, in clavis, s. stat. — Beadle in Small, Man. South. Fl. 598. 1933.

Philadelphus ser. 4. *Speciosi* (Koehne) Rehder, Man. Cult. Trees Shrubs ed. 2, 272. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949.

TYPE SPECIES: *P. inodorus* Linn.

Arching shrub with slender branchlets sweeping the ground, the bark exfoliating; leaves ovate, ovate-elliptic, elliptic, or lanceolate, dentate, rarely subentire; flowers solitary, ternate or in true dichasia; sepals foliaceous, long acuminate; petals oblong or rhomboid, rounded or obtuse at the apex; stamens 60–90; ovary with highly attached placentas, the style equal or longer than the longest stamens, the apical end divided, the stigma oar-shaped, the adaxial surfaces longer than the abaxial ones; capsules ellipsoid or subobovoid, with median persistent sepals; seeds long-caudate. Two species, many varieties. Native of the southern Appalachian region of the United States.

The type species of this section, *P. inodorus* Linn., was discovered by Mark Catesby on the bank of the Savannah River between South Carolina and Georgia. Unfortunately his artist overlooked the critical leaf characters of the plant, and instead of the faintly denticulate triplinerved leaves he depicted entire pinnate-nerved leaves. Linnaeus validated the species on the basis of Catesby's description and illustration. In trying to present a contrasting character for distinguishing this American species



MAP 2. The distribution of the sections and series of the subgenus EUPHILADELPHUS.

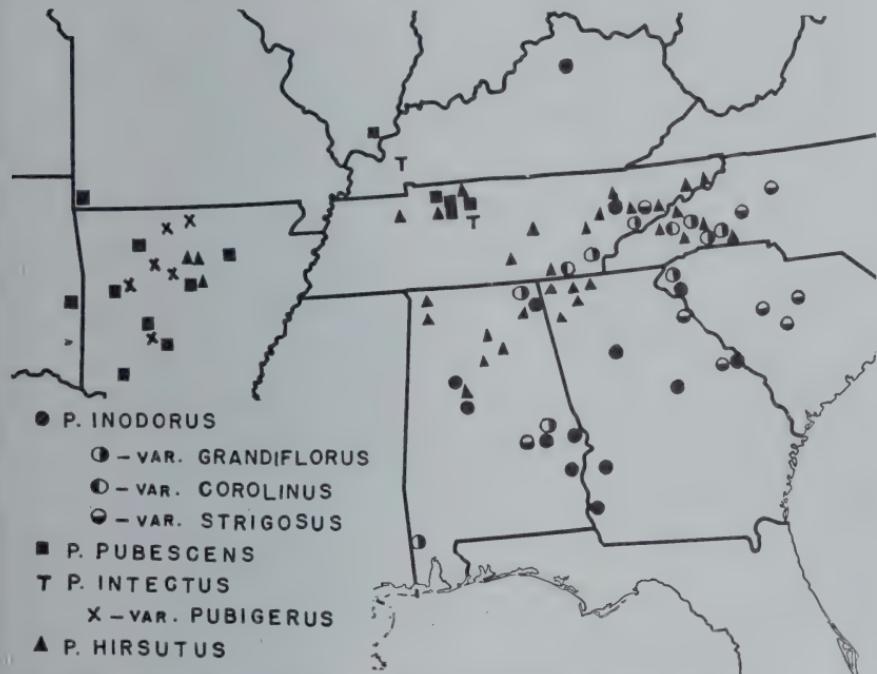
from the European one, he remarked "foliis integerrimis." Meanwhile, attempts at introducing this species from America to Europe were made. Dr. Dale in 1738 shipped both seeds and living plants to England. Miller who received this material failed to germinate the seeds. The living specimen that he planted in the Chelsea Garden was destroyed by the cold winter of 1740. There does not seem to be a successful introduction of the plant in Europe until the beginning of the nineteenth century. Thus from the time of the discovery of the first species of this section to the end of the eighteenth century the botanical records about *P. inodorus* Linn. were all from one source, that is, Catesby's Natural History of Carolina, and as a matter of fact the authors of these records, misled by the illustration, all stressed the entire leaf character of the plant. But among the natural population in this section of *Philadelphus* there is no plant that really possesses entire leaves. The leaves of some form may appear more nearly entire than the others, but leaves with small teeth actually exist on all variants, cultivated as well as the natural ones. By the beginning of the nineteenth century more plants were introduced from Carolina and Georgia to Europe under the name of *P. inodorus* Linn. As botanists were looking for an entire-leaved form to represent this binomial, the dentate-leaved material was named *P. grandiflorus* Willd. (1809), *P. laxus* Schrad. (1825), and half a dozen other synonyms as enumerated in Lavallée, Arb. Segrez. Enum. 114. 1877. The large amount of spontaneous material that I have examined convinces me that the formerly recognized species, *P. grandiflorus* Willd., and *P. laxus* Schrad., are merely different forms of a species with heterogeneous leaf shape, size and margins. Fostered by growers, propagated and distributed through cuttings, these forms have maintained their distinction in gardens since their discoveries. But when they are projected on the spectrum of variations exhibited by a large number of specimens collected from the homeland of *P. inodorus* Linn. they appear to be nothing but a few transitional forms. In this paper, these forms are treated as varieties.

Beadle in 1902 discovered a species with pubescent pedicels and hypanthia from the Coosa River region in Georgia. This discovery makes the second species of the section Pauciflorus.

This section is endemic to the southern Appalachian Mountains. The Great Smoky and the Lookout Mountains are the centers of the concentration of its species, and the Stamping Ground in Kentucky, Statesville in North Carolina, Santee River region in South Carolina, Coheelee Creek in Georgia and Mobile in Alabama mark the periphery of their overlapping ranges. The specimens collected from the cliffs on the Delaware River in Pennsylvania seem to be out of the range and they probably represent some escapes. As illustrated in Map 2, there seems to be no marked geographical separation between *P. inodorus* Linn. and *P. inodorus* Linn. var. *grandiflorus* (Willd.) Gray. *Philadelphus inodorus* Linn. var. *laxus* (Schrader) S. Y. Hu has been collected only once in nature, and that was on Great Smoky Mountain. *Philadelphus inodorus* Linn. var. *carolinus* S. Y. Hu occurs both in the Blue Ridge area of North Carolina and the

Lookout Mountains at the Georgia-Alabama-Tennessee border. *Philadelphus inodorus* Linn. var. *strigosus* Beadle is only known from the type locality and a plant cultivated in the Arnold Arboretum.

In this study, I have examined 191 specimens representing 161 collections that belong to this section, and have observed very little morphological modification which leads to speciation. This scarcity of variations apparently indicates the stability of the species of the sections.



MAP 3. The distribution of the major species of *Philadelphus* in southeastern United States.

KEY TO THE SPECIES

A. Pedicels and hypanthia glabrous 15. *P. inodorus*.
 AA. Pedicels and hypanthia pubescent 16. *P. floridus*.

15. *Philadelphus inodorus* Linn. Sp. Pl. 470. 1753.—Miller, Gard. Dict. [834]. 1768.—Walter, Fl. Carol. 146. 1788.—Willd. Sp. Pl. 2: 948. 1800.—Barton, Elem. Bot. pl. 18, fig. 1. 1803.—Michx. Fl. Bor. Am. 1: 283. 1803.—Aiton, Hort. Kew. ed. Alt., 3: 180. 1811.—Pursh, Fl. Am. Sept. 1: 329. 1814.—Elliott, Sketch 1: 538. 1821.—DC. Prodr. 3: 206. 1828.—Schrader in Linnaea 12: 401. 1838.—Loudon, Arb. Frut. Brit. 2: 952, fig. 647. 1838.—Torr. & Gray, Fl. N. Am. 1: 594. 1840.—Chapman, Fl. South. U.S. 156. 1860.—Koch, Dendr. 338. 1869.—Gray, Man. ed. 2, 146. 1856.—Lavallée, Arb. Segrez. Enum. 114. 1877.—Dippel, Handb. Laubh. 3: 333. 1893.—Koehne, Dendr. 184. 1893; in Gartenfl. 45:

507. 1896; et in *Mitt. Deutsche Dendr. Ges.* 1904(13): 80. 1904.—
 Britton & Brown, *Ill. Fl.* 2: 186, fig. 1861. 1897; ed. 2, 232, fig.
 2189. 1913.—Beadle in *Small, Fl.* 507. 1903; ed. 2, 506. 1913 et
 in *Small, Man. South. Fl.* 598. 1933.—Schneider, *Ill. Handb. Laubh.*
 1: 366. 1905.—Rydb. in *N. Am. Fl.* 22: 206. 1905.—Syereisht-
 chikof, *Ill. Fl. Mosc.* 2: 220, fig. [1.] 1907.—Standley & Calderon,
Pl. Salv. 88. 1925.—Fernald, *Gray's Man.* ed. 8, 746. 1950.—
 Gleason, *Ill. Fl.* 2: 273. 1952.

Philadelphus flore albo majore inodoro Catesby, *Nat. Hist. Car.* 2: 84, pl. 84.
 1743.

Syringa inodora Moench, *Meth.* 678. 1794.

TYPE: Catesby pl. 84. LECTOTYPE: *Harper* 3353 (A).

An arching shrub, 1–3 m. high, bark of the second year's growth castaneous, exfoliating; current year's growth glabrous. Leaves ovate-elliptic or elliptic, rarely broad elliptic, subentire, faintly dentate, 5–9 cm. long, 2–3.5 cm. wide, acute or sub-cuneate rarely obtuse at the base, short acuminate at the apex, sparsely appressed pilose, rarely subglabrous above, glabrous except the primary nerves and their angles beneath. Flowers 1, 3, rarely up to 9, cymose, the pedicels, hypanthia, and sepals all glabrous; corolla disciform, 4–5 cm. across, the petals oblong, 2 cm. long, 1.5–1.8 cm. wide; stamens 60 up to 90; style equal to the longest stamens in length, glabrous, the stigmas dilated, the abaxial surface definite. Capsules subglobose-ellipsoid, 8 mm. long, 7 mm. diameter, the seeds long-caudate.

UNITED STATES: Pennsylvania: cliffs along the Delaware River, T. C. Porter, June 29, 1885 (NY), July 11, 1886 (G). Virginia: Caroline Co., Return, *Fernald, Long & Abbe* 14168 (G); Polk Co., near Columbus Mountainside, *E. C. Townsend*, in 1897 (CU). North Carolina: without precise locality, *G. R. Vasey* in 1878 (US). South Carolina: Oconee Co., Tomasssee Knob, *H. D. House* 2070 (NY, US); Oconee County, Seneca River, *K. M. Wiegand & W. E. Manning*, August 1927 (CU). Georgia: cliffs along the Savannah River, at the Locks above Augusta, *C. S. Sargent*, March 20, 1908 (A, TOPOTYPE?); "In Georgia et Carolina circa urbem Augusta," *S. T. Olney & J. Metcalf* 122 (G); Baldwin Co., Milledgeville, *T. G. Harbison* 1549 (A); 1551 (A); Burke Co., *McBean, J. H. Pyron & R. McVaugh*, April 1938 (CU); Clarke Co., common on river banks, *J. H. Miller*, May 1925 (CU); Columbia Co., Lincolnton, Little River, *W. H. Duncan* 9496 (CU); Dekalb Co., *John Davis* 1852 (US), 7217 (BH), July 1921 (CU); Early Co., Coheelee Creek, *R. F. Thorne* 7424 (CU); Early Co., Gulf Coastal Plain, *R. F. Thorne & W. C. Muenscher* 8556 (CU); Macon Co., *I. Darby* in 1836 (NY); Steward Co., *R. M. Harper* 1089 (NY, US); without precise locality, *Dr. Boykin* (NY). Kentucky: Scott Co., Stamping Ground, *J. W. Singer* 84 (US). Tennessee: Knox Co., Knoxville, *J. N. McCarroll* 42; *A. Ruth* 256 (MO, US), 260 (NY), 345 (G), 2023 (NY), May 21, 1887 (TENN), July 15, 1900 (TENN); Rutherford Co., Murfreesboro, *E. J. Palmer* 35494 (A, MO, NY); Interior of Tennessee, without precise locality, *Herb.*

I. Carey (NY). Alabama: Dekalb Co., Mentone, *Loring* in May 1899 (US); Lee Co., Auburn, *F. S. Earle & L. M. Underwood*, April 25, 1896 (NY); Tuscaloosa Co., Brush Creek, *R. M. Harper* 3353 (A.BH, G, NY, US); same county, Black Warrior River, *R. I. & E. R. Clausen*, April 1952 (CU); same locality, *E. J. Palmer* 35362 (A.MO, NY, US), 35363 (A, NY); Holt, *H. E. Wheeler* 1318 (A); Banks of Alabama River, *R. S. Cocks* in July 1914 (A); Bank of Chattahoochee River, *Chapman* in Dec. 1867 (NY); Without precise locality, *S. B. Buckley* in June 1841 (NY); *Chapman* (NY); Herb. P. V. LeRoy (NY).

CULTIVATED: United States: Massachusetts: Arnold Arboretum no. 15347, collected on June 30, 1913 (A), Arnold Arboretum no. 5312, collected on June 12, 1918 (BH), Aug. 8, 1918 (BH); Hort. Bot. Cambridge, *A. Rehder*, June 29, 1907 (A); Jamaica Plain, *C. E. Faxon*, June 20, 1911 (A). New York: Normal College Ground, *A.R.R.* on June 4, 1889 (NY). New Jersey: Somerset Co., Watchung, *H. N. Moldenke* 1690 (NY), 2515 (BH). Pennsylvania: Delaware Co., Media, *F. W. Pennell* 12976 (NY). Washington D. C.: U. S. Dept. Agri. Ground, *B. Sudworth*, May 18, 1891 (US), May 22, 1891 (US); *G. Vasey* in 1873 (US), in 1882 (US); Maryland Agri. College, *G. Vasey* in 1873 (US); Rock Creek, *L. F. Ward*, May 30, 1883 (US), May 20, 1886 (US). Missouri: Marion Co., Hannibal, Riverside Cemetery, *J. Davis* 2306 (MO). Wisconsin: Green Bay, *J. H. Schuette* (NY).

Philadelphus inodorus has been much misinterpreted in botanical literature because of the over emphasis of various authors on the margin of the leaves and their disregard of the shape and base of the leaves and the flower characters as illustrated in Catesby's plate. Among modern collections made from southeastern United States, Catesby's illustration of the flowering and fruiting branchlets of the species is duplicated in *Palmer* 25362, 35494, *Harbison* 1551 and *Harper* 3353, the last mentioned specimen deposited in the herbarium of the Arnold Arboretum has been selected as the lectotype for the species.

Judging from the specimens which I have examined, the Great Smokies is the center of concentration of this species. The specimens from eastern Pennsylvania, eastern Virginia, northern Kentucky and the Gulf Coastal Plain in Georgia either mark the periphery of its natural range or they were collected from escaped plants. The available field notes indicate that the habitats of *P. inodorus* Linn. are steep wooded slopes, banks of rocky streams or limestone bluffs. Duncan recorded the plant as attaining a height of eleven feet. The stems are slender and arching. The natural population flowers in middle April or early May in Georgia and Alabama. The cultivated ones bloom in middle June in Boston. Regarding the habit, Catesby remarked the plant being a small tree, rising to a height of about sixteen feet or upwards with a slender trunk. As far as I know all species of *Philadelphus* are shrubs. Catesby's remark was either due to his loose concept of the term tree or due to the crowded condition in which that particular plant grew with no chance to branch at the base.

KEY TO THE VARIETIES AND FORMS OF *P. INODORUS*

A. Sepals glabrous outside.

B. Leaves ovate-elliptic, elliptic or lanceolate, the base obtuse, acute or cuneate; remotely coarse-toothed.

C. Leaves ovate-elliptic; corolla discoid.

D. Half-open flower campanulate, the petals first suborbicular, later oblong 15a. var. *grandiflorus*.

DD. Half-open flower quadrangular, the petals first rhomboid, later orbicular 15b. forma *quadranguliflora*.

CC. Leaves elliptic or lanceolate; corolla cruciform 15c. var. *laxus*.

BB. Leaves ovate, the base rounded; margin faintly denticulate or semi-entire 15d. var. *carolinus*.

AA. Sepals with few hairs on the outside 15e. var. *strigosus*.

15a. *Philadelphus inodorus* var. *grandiflorus* (Willd.) Gray, Man. ed. 2, 146. 1856; ed. 4, 146. 1865; ed. 5, 166. 1867.—A. Wood, Am. Bot. Flor. 116. 1879.—Nemoto, Fl. Jap. Suppl. 294. 1936.—Fernald, Gray's Man. ed. 8, 746. 1950.

Philadelphus grandiflorus Willd. Enum. Pl. Hort. Bot. Berol. 511. 1809.—DC. Prodr. 3: 206. 1828.—Elliott, Sketch 1: 538. 1821.—Schrader in Linnaea 12: 395. 1838.—Sweet, Brit. Fl. Gard. ser. 2, 1: pl. 8. 1829.—Loudon, Arb. Frut. Brit. 2: 954. 1838.—Torr. & Gray, Fl. N. Am. 1: 595. 1840.—Walp. Rep. 2: 151. 1843.—Young, Fl. Texas 290. 1873.—Lavallée, Arb. Segrez. Enum. 115. 1877.—Britt. & Brown, Ill. Fl. 2: 186, fig. 1862. 1897.—Nicholson, Ill. Dict. Gard. 3: 95. 1886.—Watson & Coulter, Gray's Man. ed. 6, 174. 1890.—Nicholson, Kew Hand-list 1: 225. 1894, ed. 2, 375. 1902.—Schneider, Ill. Handb. Laubh. 1: 366, fig. 234g-j, 236e. 1905.—Rydb. in N. Am. Fl. 22: 168. 1905.—Rehder, Man. Cult. Trees Shrubs 278. 1927; ed. 2, 272. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949.—Bean in Chitt. Dict. Gard. 3: 1546. 1951.

Philadelphus speciosus Schrader ex DC. Prodr. 3: 206. 1828; et in Linnaea 12: 43. 1838.—Koehne, Dendr. 184. 1893; in Gartenfl. 45: 507. 1896; et in Mitt. Deutsche Dendr. Ges. 1904(13): 80. 1904.

Philadelphus macranthus Jacques in Hort. Univ. 2: 17. 1841.

Philadelphus gloriosus Beadle in Biltm. Bot. Stud. 1: 159. 1902; in Small, Fl. 507. 1903, ed. 2, 506. 1913; et in Small, Man. South. Fl. 599. 1933.—Rydb. in N. Am. Fl. 22: 169. 1905.—Schneider, Ill. Handb. Laubh. 1: 366. 1905.

Philadelphus columbiensis Hort. ex Nicholson, Kew Hand-list 1: 225. 1894, ed. 2, 375. 1902, nomen nudum.

Deutzia sanguinea Hort. ex Nicholson, ll. cc.

Philadelphus inodorus sensu Gleason, Ill. Fl. 2: 273. 1952, pro parte, non Linn.

TYPE: Cultivated plant in the Botanical Garden of Berlin. LECTOTYPE: Biltmore Herb. No. 4333a, from rocky banks of Grand River, Rutherford County, North Carolina, deposited in Herbarium, Arnold Arboretum.

A mound-like shrub with slender arching branchlets, bark of two-year old growth castaneous, exfoliating; leaves ovate or ovate-elliptic, 5–11 cm. long, 2.5–5, sometimes up to 6.5 cm. wide, glabrescent or very sparsely strigose on both surfaces, bearded in the axils of primary nerves beneath, denticulate, the teeth usually coarse and remote, acute or rarely rounded at the base, acuminate at the apex; flowers ternate, solitary, or 7–9 in a true dichasium, pedicels 3–15 mm. long; sepals ovate, 8–12 mm. long, 5–6 mm. wide, acuminate; corolla campanulate at first, later semidisciform, 4–5.5 cm. across, the petals suborbicular, becoming oblong, 20–26 mm. long, 15–22 mm. wide; capsules ellipsoid, 12–15 mm. long, 6–9 mm. in diameter.

UNITED STATES: Virginia: Without precise locality, *Stebbins* (NY). North Carolina: Buncombe Co., Blue Ridge, *A. Gray* in 1843 (NY); Polk Co., Skyuka Mt., *J. R. Churchill*, May 25, 1899 (BH), same county, Pacolet River, *J. R. Churchill*, May 29, 1899 (BH, TENN); Rutherford Co., rocky banks of Grand River, near Chimney Rock, *Biltmore Herb.* 4333a (A, NY, US); same county below Hickory Falls, *Correll, Blomquist & Garren* 5140 (A); mountains of North Carolina, *G. R. Vasey* in 1878 (NY); Hickory Mt. Gap, *Gray* (NY); Rutherford Gap, *S. B. Buckley*, August 1841 (NY). South Carolina: Oconee Co., along streams and rivers, *A. P. Anderson* 1173 (US); Tomassee Knob, *H. D. House* 2056 (NY, US); Clemson College 2116 (NY, US). Georgia: Dade Co., Lookout Mt., *E. J. Palmer* 35446 (A, MO); Lookout Mt. between Tennessee and Georgia, *J. R. Churchill*, April 30, 1906 (TENN), May 3, 1906 (BH); Macon, Ocumulgee River Swamp, *J. K. Small*, May 18–24, 1895 (NY), July 8–9, 1895 (A); Rome, cliffs of Cossa, *T. G. Harbison* 39 (A); same area, Black's Bluff, *Alexander, Everett & Pearson*, Oct. 1933 (NY); Sugalo River near its juncture with Senesa, *L. R. Gibbs* in 1885 (NY); Wilkes Co., Little River, *T. G. Harbison*, July 14, 1919 (A, US); without precise locality, *Herb. Chapman*, 878 (US); Benton Co., Rockport, *E. B. Harger* 7892(G). Tennessee: Polk Co., *Sharp, Adams & Felix* 11406 (A, TENN); Sevier Co., *H. M. Jennson* 1208 (TENN). Alabama: Lee Co., Auburn, *E. T. Earle*, April 25, 1896 (US); Jackson Co., Bridgeport, *Biltmore Herb.* No. 4333e (NY); Lisbon, *C. Mohr*, July 24, 1885 (US); Mobile Co., Mobile, *E. Smith* in 1891 (A, US).

CULTIVATED: Europe: Germany: Hort. Götting, *A. Rehder* 387 (A), 1644 (A); *Schrader* in 1827 (TYPE of *P. speciosus* Schrader; photograph, A). England: Kew, *Geo Nicholson* 1316 (A). Asia: China: Shanghai, St. John's University, *L. H. Bailey*, May 14, 1917 (BH), May 23, 1917 (BH).

The plant cultivated in Shanghai is reported by Bailey as producing fragrant flowers.

Willdenow characterized *P. grandiflorus* by the ovate, acuminate, and dentate leaves which were fasciculate pilose in the principal nerve-angles beneath. He remarked that the plant was introduced to the Botanical Garden of Berlin as *P. inodorus*. Willdenow's concept of the species had been adopted by European botanists outside Germany for over a half century without questioning. Koch and Koehne, two outstanding German students of the genus, never accepted Willdenow's species. On observa-

tion of spontaneous material Gray found the characters used by Willdenow to be unreliable for specific distinctions and in 1856, in the second edition of his Manual of Botany, he treated Willdenow's species as a variety of *P. inodorus* Linn. This trinomial existed in Gray's Manual for over thirty years in four different editions. In 1890 when Watson and Coulter revised Gray's Manual, they re-established Willdenow's species for no obvious reasons. Meanwhile, Britton and Brown tried to distinguish *P. grandiflorus* Willd. from *P. inodorus* Linn. on the strength of the relative length of the calyx lobes, and on their geographical distribution. These authors maintained that *P. grandiflorus* Willd. had calyx lobes about twice as long as the tube and that it occurred on low ground from Virginia to Tennessee and Florida while *P. inodorus* Linn. had calyx lobes equalling the tubes and occurred principally in the mountains, from Virginia to Georgia and Alabama. This character, the proportion of sepals and hypanthium, had also been adopted for distinguishing *P. grandiflorus* Willd. and *P. inodorus* Linn. by Rydberg and Beadle. Gleason in 1952 maintained that the observations that these authors had made were not substantiated on an examination of the plant. Swinging to the other extremity, he amalgamated the two species. Fernald in 1950, in the eighth edition of Gray's Manual adopted Gray's concept, and I think he is justified in so doing.

Jacques in 1841 described a plant cultivated as *P. inodorus* in the garden of M. Bertin and named it as *P. macranthus*. He characterized that plant as having ovate-elliptic or ovate-oblong dentate leaves which are narrowed at the base, and ternate large flowers with rounded petals. Judging from his description the plant he saw must belong to *P. inodorus* var. *grandiflorus*.

Britton and Brown and Small all claimed the taxon to occur in Florida. I have seen no spontaneous specimens from that state.

Schrader in 1828 described *P. speciosus* as a plant possessing an 8-celled ovary. His illustration indicated that the cross section he made was cut through the tip of a young fruit. Due to a partial false septa projecting from the roof of each cell of the ovary such a cross section would appear 8-celled. Through the courtesy of Dr. Charles Baehni, Director of the Conservatoire et Jardin Botaniques, Genève, I have the photocopies of the original drawings and the text of Schrader's manuscript as well as the photographs of the types of Schrader's species. By the help of one of the curators of the same institution, Mr. Weibel, I received a careful description of the indumentum of the floral parts, including the hypanthium, sepals, petals, styles and disk, of all Schrader's species. I have no doubt that *P. grandiflorus* Willd. and *P. speciosus* Schrader are conspecific.

Beadle in 1902 on the strength of an abrupt contraction of the base of the capsule described *P. gloriosus* from the banks of the Coosa River near Rome in Georgia. The degree of fullness of a capsule has a profound effect on the appearance of the base of the fruit in *Philadelphus*. I have

examined many collections from the Coosa River region and found no fruit character distinctive specifically. Beadle's material appears to have fuller fruits.

15b. *Philadelphus inodorus* Linn. var. *grandiflorus* (Willd.) Gray
· *forma quadranguliflorus*, f. nov.

Frutex erectus, ramis pendulis, bienniis 5 mm. diametro, corticibus exfoliatis, hornotinis glabris; foliis oblongo-ovatis vel ovatis, 3–10 cm. longis, 1.5–5 cm. latis, basi obtusis vel rotundatis, apice acuminatis, subtiliter remoto-serratis vel subintegris, supra glabris vel adpresso-pilosis, subtus ad nervis primariis villosis barbatisque; flores 1 vel 3, raro usque ad 9, cymosis, corolla quadrangulari, petalis orbicularibus, 2.2 cm. longis, 2.6 cm. latis.

UNITED STATES: North Carolina: Rutherford Co., bank of the Broad River near Chimney Rock, Biltmore Herb. No. 6555 (NY). South Carolina: Kershaw Co. near Camden, along Wateree River, *E. J. Palmer* 39949 (A). Georgia: Rome, cliffs of Coosa River, *C. S. Sargent*, May 6, 1899 (A, TYPE).

CULTIVATED: Germany: Hort. Götting. *A. Rehder* 388 (A), 1672 (A). U.S.A.: Arnold Arboretum No. 5312, *C. E. Faxon* June 14, 1911 (A), June 16, 1911 (A). Arnold Arboretum No. 4159-2, collected on August 8, 1918 (BH); Arnold Arboretum No. 15340, collected on Oct. 3, 1916 (A); Arnold Arboretum No. 15357, collected on June 20, 1904 (A). New York: Rochester, Highland Park, *R. E. Horsey*, July 17, 1918 (BH), Sept. 4, 1918 (BH).

This form can easily be recognized by its square flowers, the petals are always broader than long and they overlap each other at anthesis. It was probably first introduced by Sargent from Georgia and distributed under the name *P. grandiflorus*. The broad petals of the flowers are very distinctive, and when the flowers first open, they appear square.

15c. *Philadelphus inodorus* var. *laxus*, comb. nov.

Philadelphus laxus Hort. ex Schrader in DC. Prodr. 3: 206. 1828; et in Linnaea 12: 398. 1838.—Loudon, Arb. Frut. Brit. 2: 954, fig. 677. 1838.—Lindl. in Bot. Reg. 25: pl. 39. 1839.—Lavallée, Arb. Segrez. Enum. 115. 1877.—Koehne, Dendrol. 184. 1893; in Gartenfl. 45: 507. 1896; et in Mitt. Deutsche. Dendrol. Ges. 1904(13): 79. 1904.—Rydb. in N. Am. Fl. 22: 174. 1905.—Schneider, Ill. Handb. Laubh. 1: 365. 1905.—Rehder, Man. Cult. Trees Shrubs 278. 1927; ed. 2, 272. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949.—Bean in Chitt. Dict. Gard. 3: 1546. 1951.

Philadelphus grandiflorus Willd. var. *laxus* (Schrader) Torr. & Gray, Fl. N. Am. 1: 595. 1840.—Walp. Rep. 2: 151. 1843.—Nicholson, Kew Hand-list 1: 225. 1894; ed. 2, 375. 1902; et Ill. Dict. Gard. 3: 95. 1886.—Anon. in Garden 40: 289. 1891.—Raffil. in Gard. Chron. III. 43: 82, fig. 36: 1908.

Philadelphus humilis hort. ex Schrader in DC. Prodr. 3: 206. 1928, in syn.

Philadelphus ignea Hort. ex Nicholson, Kew Hand-list 1: 225, 1894, in syn.

Philadelphus pubescens Lodd. Cat. ed. 16, 1836, nomen nudum. — Loudon, Arb. Frut. Brit. 954. 1938, in syn., non Loisel., 1820.

TYPE: Schrader, (Conservatoire et Jardin Botaniques, Genève).

A mound-like shrub with arching branches, the branchlets slender, pendulous, touching the ground, the bark of second year's growth exfoliate; leaves lanceolate or elliptic-lanceolate, 4–6 cm. long, 1.5–2.5 cm. wide, cuneate or acute at the base, acuminate at the apex, glabrescent or sparsely appressed pubescent above, sparsely pubescent beneath, especially along the principal nerves; beard in the nerve-axils, the margin remotely fine serrate, rarely subentire; flowers 4.5–5.5 cm. in diameter, corolla cruciform, the petals oblong, 2.3 cm. long, 1.5 cm. wide.

UNITED STATES: North Carolina: Swain Co., Nantahala Gorge; K. M. Wiegand, June 1931 (CU).

CULTIVATED: Europe: Switzerland, Botanical Garden of Geneva, Schrader (TYPE of *P. laxus* Schrader, photo in A); without collector, June 1826 (NY). Germany: ex. Herb. Dendrol. Koehne 18 (MO); Hort. Bot. Jena, A. Rehder, June 1895(A); Hort. Mund, A. Rehder 2256 (A), 2268 (A); Hort. Musk, A. Rehder, July 2, 1888 (A); Hannover, Bot. Garten Forstakadamie, H. Zabel, June 13, 1894 (A). Austria: Hort. Bot. Wien, C. Schneider, June 6, 1902 (A). France: Segrez. Lavallée's Arboretum, June 16, 1907 (A); Les Barres, Vilmorin's Arboretum No. 7110, June 17, 1901 (A). United States: Boston: Arnold Arboretum No. 15353B, R. B. Clark (BH); New York: New York City, M. Ruger (NY); Rochester Highland Park, R. E. Horsey, June 16, 1918 (BH), Sept. 21, 1917 (BH); Ithaca, Bailey, July 5, 1916 (BH). North Carolina: Biltmore, W. H. Manning (BH). Tennessee: Chilhowee Park, L. D. Greenwood 2 (TENN). Arkansas: Hot Springs, E. J. Palmer 24869 (MO).

Schrader described *P. laxus* from a plant cultivated in the Botanical Garden of Geneva, and characterized it as having dentate leaves, which were pubescent beneath, and having solitary or ternate flowers. He gave as the origin of that taxon North America. A specimen in the Herbarium of the New York Botanical Garden which was distributed by the Geneva Botanic Garden under the name *Philadelphus inodorus* matches Schrader's plate and the photograph of his type in every respect. It was collected in June 1826. As Schrader finished his work in 1827, this specimen was probably collected from the type plant at the time when Schrader made his studies. This specimen is identical with Wiegand's collection made in Nantahala Gorge of North Carolina. Incidentally Wiegand's collection represents the only specimen that I have examined which is not marked "cultivated." This variety differs from typical *P. inodorus* Linn. only in its narrower leaves which are sparsely pubescent beneath. As this leaf-character is not specifically distinctive, I therefore treat Schrader's species as a variety of *P. inodorus* Linn.

In the Vilmorin Arboretum, Les Barres, France, a mistake was once made in recording the origin of a plant. A tag labeled "P. spec. China No. 1505" was attached to a *laxus* type of *Philadelphus*. A specimen from that plant was sent to Koehne, who accordingly in 1904 advanced a sup-

position that *P. laxus* Schrader was endemic to China, specifically Szechuan Province. In so doing Koehne overlooked the fact that at that early period, Szechuan, being situated in the interior region, was not accessible to Europeans. As Bretschneider remarked that during the eighteenth century and the early half of the nineteenth century, Canton was the only Chinese port open to European trade,¹ and *Philadelphus* does not grow in Canton, either in a wild state or in cultivation, it was highly impossible for such a plant to be introduced to Europe from China.

In the European gardens *P. inodorus* Linn. var. *laxus* S. Y. Hu existed under different binomials some of which also appear as synonyms of *P. lewisii* Pursh and *P. hirsutus* Nutt.

Torrey and Gray in 1840 interpreted Schrader's species as a variety of *P. grandiflorus* Willd. It is true that these two taxa are closely related, especially when the remotely coarse dentate leaves are considered. In this study they are both treated as varieties of *P. inodorus* Linn. The var. *grandiflorus* is distinguished by its broad ovate leaves and discoid corolla and var. *laxus* by its lanceolate or elliptic-lanceolate leaves and cruciform corolla.

15d. *Philadelphus inodorus* Linn. var. *carolinus* var. nov.

Philadelphus inodorus sensu Sims in Bot. Mag. 36: pl. 1478. 1812. — Lavallée, Arb., Segrez. Enum. 114. 1877. — Rehder, Man. Cult. Trees Shrubs 278. 1927, ed. 2, 272. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949. — Bean, Trees, Shrubs, ed. 7, 2: 414. 1950; et in Chitt., Dict. Gard. 3: 1546. 1951, non Linn. 1753.

Philadelphus columbarius myrtiflorus Hort. ex Lavallée, Arb. Segrez. Enum. 114. 1877., in syn.

Philadelphus cordatus Hort. ex Lavallée, l. c., in syn.

Philadelphus cordifolius Hort. ex Lavallée, l. c., in syn.

Philadelphus coronarius nivalis Hort. ex Lavallée, l. c., in syn.

Philadelphus multiflorus Hort. ex Lavallée, l. c., in syn.

Philadelphus floribundus Hort. ex Lavallée, l. c., in syn., non Schrader, 1828.

Philadelphus grahami Hort. ex Lavallée, l. c., in syn.

Philadelphus zeyheri multiflorus Hort. ex Lavallée, l. c.

Frutex humilis, ramis pendulis, bienniis 2–4 mm. diametro, corticibus exfoliatis, hornotinis glabris; foliis subcoriaceis, integris vel subintegris, ovatis, 3.8 cm. longis, 2–4 cm. latis, basi rotundatis vel raro obtusis, apice breviter acuminatis, glabris vel supra sparse adpresso-pilosus et subtus ad nervis pilosis barbatisque; flores 1, vel 2, raro 3 usque ad 9, 4–6 cm. diametro, petalis suborbiculo-ovatis; staminibus 63 usque 90.

UNITED STATES: North Carolina: without precise locality, *G. R. Vasey* in 1878 (TYPE, US); Chimney Rock, *Alexander, Everett & Pearson*,

¹ E. BRETSCHNEIDER, History of European Botanical Discoveries in China, 155–156. 1898.

Sept. 27, 1933 (NY). Tennessee: Hamilton Co., Chattanooga, Ledges Jonas Bluff, Lookout Mountain, S. R. Churchill 449 (TENN.).

CULTIVATED: Biltmore Herb. No. 7610 (A, G, MO, NY, US); Arnold Arboretum, S. Y. Hu, June 8, 1951 (A), July, 1952 (A); Arnold Arboretum No. 540-2, (Plant collected near Chimney Rock N. C.) A. Rehder on June 16, 1903 (MO). Arnold Arboretum No. 4159-1, collected on June 19, 1889 (A), June 26, 1902, June 28, 1904, June 14, 1911, June 23, 1916, June 26, 1916, Oct. 3, 1916 (All in A); Massachusetts Agricultural College, C. H. Thompson, June 7, 1921 (MO).

This variety is characterized by its ovate leaves with rounded or obtuse base and faintly denticulate or subentire margins. In nature it has very limited range of distribution. The material that I have examined all come from the mountains of western North Carolina and the adjacent southeastern Tennessee. The cultivated specimens in large American herbaria apparently all come from two sources, the one from a plant originally transplanted from the bank of the Flint River in Georgia by the Biltmore Herbarium (No. 7610), and the other from a plant originally transplanted from Chimney Rock in North Carolina as represented by the Arnold Arboretum field No. 540-2.

The introduction of this variety to European gardens was made about 1810. In 1812 a flowering specimen was presented to Sims by Whitley of the Fulham Nursery. A colored plate was prepared from this specimen and was published under the name *P. inodorus*. A comparison of this plate with that of Catesby's reveals that those plates represent two different elements. That of Catesby depicts a plant with ovate-lanceolate leaves and oblong petals which are rounded at the apex and that of Sims' illustrates a plant with broad ovate leaves and semirhomboid petals obtuse at the apex. In this work the plant that Catesby illustrated is interpreted as the true *P. inodorus* Linn. while the plant that Sims described is identified as *P. inodorus* Linn. var. *carolinus* S. Y. Hu. Lavallée named his plant with the help of Sims' publication, thus the synonyms he listed under *P. inodorus* in the Arboretum Segrezianum are placed here as the synonyms of this variety. Rehder relied on a plant cultivated in the Arnold Arboretum for the description of *P. inodorus* in his Manual. As that plant is not a genuine *P. inodorus* Linn., Rehder's description applies only to this variety.

15e. *Philadelphus inodorus* Linn. var. *strigosus* Beadle in Biltm. Bot. Stud. 1: 159. 1902; in Small, Fl. 507. 1903, ed. 2, 506. 1913; et in Small, Man. South. Fl. 598. 1933.—Schneider, Ill. Handb. Laubh. 1: 366. 1905.

Philadelphus strigosus (Beadle) Rydb. in N. Am. Fl. 22: 168. 1905.

Philadelphus laxus Schrader var. *strigosus* (Beadle) Rehder in Jour. Arnold Arb. 1: 198. 1920; Man. Cult. Trees Shrubs 278. 1927; ed. 2, 272. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949.

TYPE: *A. C. Hexamer & F. W. Maier*, June 19, 1855 (G).

A straggling shrub up to 2 m. high, bark castaneous, exfoliating; leaves ovate or ovate-elliptic, 3–7 cm. long, 2–4 cm. wide, subentire, or faintly denticulate, obtuse or rounded at the base, acuminate at the apex, glabrous or partially sparsely strigose above, uniformly strigose beneath, bearded at the nerve-angles; flowers solitary or ternate, the pedicels and hypanthia glabrous, the sepals ovate, 8 mm. long, 5 mm. wide, sparsely villose on the outside; corolla disciform, 4–5 cm. across, the petals suborbicular, 2 cm in diameter; stamens about 90, the longest 1 cm. long; style as long as the longest stamens, the abaxial surface of the stigma 3 mm. long.

UNITED STATES: North Carolina: Burke Co., Tablerock, *H. D. Hasse* (NY); Iredell Co., Statesville, *M. E. Hyais* 4986 (NY), May 1881 (NY). South Carolina: Kershaw Co., near Camden, *E. J. Palmer* 39949 (NY, US); Lexington Co., *A. C. Hexamer & F. W. Maier*, June 19, 1855 (TYPE G); Santee River, *M. Tuomey* (NY); without precise locality, *M. A. Curtis* (MO). Georgia: Richmond Co., above August, *S. T. Olney & J. Metcalf*, April 1855 (NY); same area, at the Locks, *C. S. Sargent* on June 20, 1908 (A); Elbert Co., *T. G. Harbison* 16 (A). Tennessee: Servier Co. *H. M. Jennison* 367 (TENN). Alabama: Montgomery Co., Montgomery, *O. L. Justice*, April 20, 1941 (CU).

CULTIVATED: Europe: Bernhard Herb (MO). U.S.: Washington: Sequim, *J. M. Grant*, June 6, 1913 (NY). Missouri: St. Louis, Missouri Bot. Gard., *J. H. Kellogg*, May 21, 1902 (CU).

Beadle was justified in treating this taxon as a variety of *P. inodorus* Linn. for it differs from the genuine species only in its thicker covering of appressed, rather stiff hairs on the lower surface of the leaves and on the exterior of the sepals. Like *P. inodorus* Linn. it has glabrous pedicels and hypanthia. In the texture, shape, and margin of the leaves, much variation exists among the specimens cited above. So far as my records go, the earliest collection was made not long before 1847 by M. A. Curtis from South Carolina. It was presented to Engelmann in 1847 under the name *P. grandiflorus* Willd. The first cultivated record that I have seen is represented by some specimens of the Bernhard Herbarium. They were then cultivated in Europe under the name *P. inodorus* Linn. or *P. laxus* Schrad.

16. **Philadelphus floridus** Beadle in Biltm. Bot. Stud. 1: 160. 1902; in Small, Fl. 507. 1903; ed. 2, 506. 1913; et in Small, Man. South Fl. 599. 1933.—Schneider, Ill. Handb. Laubh. 1: 366. 1905.—Rehder in Jour. Arnold Arb. 1: 198. 1920; Man. Cult. Trees Shrubs 279. 1927; ed. 2, 273. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949, pro parte.

Philadelphus speciosus sensu Lindl. in Bot. Reg. 23: pl. 2003. 1837.—sensu Rydb. in N. Am. Fl. 22: 169. 1905, non Schrader ex DC. 1828.

Philadelphus magnificus sensu Rehder, Man. Cult. Trees Shrubs 278. 1927, ed. 2, 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949, pro parte, non Koehne.

TYPE: Biltmore Herb. No. 11376, a flowering specimen, collected on May 3rd, 1899.

Shrub up to 3 m. high, branchlets brown, the second year's growth castaneous. Leaves ovate-elliptic or broad-elliptic, 4-10 cm. long, 2-6 cm. wide, rounded or obtuse at the base, abruptly acuminate at the apex, subentire or inconspicuously remote-serrulate, very sparsely short strigose above, uniformly strigose-villose beneath. Flowers ternate, rarely solitary, or racemose with the subsequent pairs in the axils of normal leaves, the pedicels 3-7 mm. long, glabrous or sparsely villose; hypanthia and calyx sparsely villose; sepals ovate, 7-9 mm. long, 5-7 mm. wide, acuminate; corolla disciform 4-5 cm. across, the petals suborbicular, 2-2.5 cm. in diameter; stamens 80-90, the longest 1.5 cm. long, disc glabrous, the style 15 mm. long, the stigma oar-shaped, the abaxial surface definite, 1.5 mm. long; the adaxial surface 2 or 3 times longer, diminishing gradually. Capsules ellipsoid, 1 cm. long, 9 mm. in diameter, the persistent sepals supermedian. Seeds long-caudate.

UNITED STATES: Georgia: Floyd Co., near Rome, cliffs of Coosa River, Biltmore Herb. No. 11376, flowering specimen, collected on May 3, 1899 (TYPE, photo, A, NY); same number, fruiting specimen, collected on Sept. 22, 1902 (A, NY).

CULTIVATED: Europe: England: Hort. Cantab., Pl. Loddiges in 1849 (NY). Germany: Hort. Späth ex Herb. Dendr. Schneider (A). United States: Massachusetts: Hort. Bot. Cambridge, R. Cameron, June 7, 1918 (A); Hort. Dixwell, A. Rehder, June 24, 1903 (A). Canada: Dominion Arboretum and Botanic Garden, J. M. Gillett, July 3, 1939 (A).

Lindley in 1837 prepared an illustrated account about a plant which was grown in the garden of the London Royal Horticultural Society under the name *P. grandiflorus* and he named it as *P. speciosus* Schrader. Besides reprinting Schrader's original description he made no effort to characterize that plant. From his figures we know that his plant has pubescent hypanthia and calyx, a disciform corolla with suborbicular petals. As Schrader's *P. speciosus* has glabrous hypanthia and calyx, I judge that Lindley's specimen could not be Schrader's species. To ascertain the identity of the plant which Lindley called *P. speciosus* we have to turn to his discussion for some light. In the first paragraph of his discussion he admitted that "it is hardly possible to procure the species, as defined by Professor Schrader, with certainty from the nurseries, unless from Messrs. Loddiges." In the New York Botanical Garden collection there is a specimen labeled "*P. speciosus* e. pl. Loddige." This specimen has sparsely villose hypanthia and calyx. In the form and dentation of the leaves, in the type of inflorescences, in the size of the flower and in the shape of the corolla this specimen matches Lindley's illustrations perfectly.

There is no doubt that this element was what Lindley called *P. speciosus*. It is identical with the flowering type of *P. floridus* Beadle. In preparing volume 22 of the North American Flora, Rydberg had examined this specimen. He was correct in interpreting Lindley's *P. speciosus* and Beadle's *P. floridus* as conspecific. As stated above that which Lindley interpreted as *P. speciosus* was not Schrader's species. Beadle's binomial is the oldest for this taxon.

The earliest record of its cultivation in American gardens can be drawn from two collections made by A. Rehder on June 24, 1903 in the Dixwell Garden in Jamaica Plain, Mass. Later it was also cultivated in the now extinct Cambridge Botanical Garden. The later specimen was interpreted by Rehder as *P. magnificus*.

P. floridus Beadle is closely related to *P. inodorus* var. *grandiflorus* (Willd.) Gray. It can be distinguished from the latter taxon by the sparsely villose hypanthia and calyx, the uniformly strigose-villose lower leaf-surfaces and the rather frequent presence of a pair of flowers in the axils of normal leaves below the terminal ternate flowers. Those characters which distinguish it from *P. inodorus* var. *grandiflorus* are also characters which link its relationship to *P. pubescens* Loisel. It is perhaps a natural hybrid of the two. Geographically this species falls into the range of *P. inodorus* var. *grandiflorus*, but its occurrence is rare. It is only known in nature by the type collections.

There are two cultivated varieties which differ from the genuine *P. floridus* by their solitary flowers, denser pubescence and smaller leaves.

KEY TO THE VARIETIES OF *P. FLORIDUS*

- A. Leaves 4-5 cm. long, subentire or inconspicuously remote-serrulate; hypanthia sparsely strigose-villose, the underneath tissue visible; corolla cruciform 16a. var. *faxonii*.
- AA. Leaves 6-8 cm. long, prominently remote-denticulate; hypanthia densely strigose-villose, the underneath tissue obscure, corolla disciform 16b. var. *rehderiana*.

16a. *Philadelphus floridus* var. *faxonii* Rehd. in Jour. Arnold Arb. 1: 199. 1920; Man. Cult. Trees Shrubs 279. 1927; ed. 2, 273. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949.

TYPE: *C. E. Faxon*, June 28, 1907.

A graceful shrub, the bark castaneous, exfoliating; leaves elliptic, 2.5-5 cm. long, 1-2 cm. wide, obtuse or acute at the base, acuminate at the apex, subentire or faintly serrulate, glabrescent above, uniformly strigose beneath; flowers solitary or ternate, the hypanthia and calyx strigose-villose, the underneath tissue visible, the sepals ovate, 7 mm. long, 3 mm. wide, the corolla cruciform, 4 cm. across, the petals oblong, 1.8 cm. long, 1.5 cm. wide.

CULTIVATED: Boston, Mass. Hort. H. Chandler, *C. E. Faxon*, June 28, 1907 (A, TYPE); from the same plant, *C. E. Faxon*, June 16, 1911 (A).

This variety differs from typical *P. floridus* Beadle in having smaller leaves and cruciform corolla. In general appearance this variety resembles *P. inodorus* var. *laxus* (Schrader) S. Y. Hu. From the latter taxon it can readily be distinguished by its strigose-villose hypanthia and calyx. It is only known by collections made from the type plant. The Arnold Arboretum No. 10978 labeled as *P. floridus* var. *faxonii* is said to have been propagated through cuttings made from H. Chandler's garden. But the Arboretum Plant has completely glabrous hypanthia and calyx and disciform corolla with semidouble petals. It is not the genuine *P. floridus* var. *faxonii* Rehder.

16b. *Philadelphus floridus* var. *rehderianus*, var. nov.

Frutex 2 m. altus, ramis tenuibus, biennis castaneis, exfoliatis, hornotinis glabris; foliis ovatis 5–10 cm. longis, 2.5–5 cm. latis, basi acutis vel obtusis, apice acuminatis, supra sparse pilosis, subtus praesertim dense villosis, remote denticulatis; floribus solitariis, raro ternatis, pedicellis 3–8 mm. longis, dense villosis, hypanthiis calycibusque dense villosis, sepalis ovatis, 9 mm. longis, 5 mm. latis, corolla disciformi, 4–5 cm. diametro, petalis suborbicularibus, ca. 2 cm. diametro; staminibus ca. 90, 3–12 mm. longis; stylo cum stigmatibus 14 mm. longo; capsulis ellipsoideis, 10–11 mm. longis, 8–9 mm. diametro.

CULTIVATED: Arnold Arboretum No. 5311, A. Rehder, June 18, 1910 (TYPE, A); C. E. Faxon, June 14, 1911 (A), Oct. 3, 1916 (A); C. K. Allen, June 21, 1927 (A).

This very distinct form was introduced into cultivation through the Arnold Arboretum in 1906. It was raised from seeds collected from Highland, North Carolina by T. G. Harbison. In appearance it resembles *P. inodorus* var. *grandiflorus* f. *quadranguliflorus* S. Y. Hu. It can be readily distinguished from the latter form by its densely pubescent hypanthia and calyx and its uniformly dense pubescent lower leaf-surfaces.

The above cited specimens have been named by Rehder as *P. floridus*. The type of Beadle's species has very sparsely villose hypanthia and calyx and subentire or faintly serrulate leaves. The indumentum of the hypanthia and calyx of this variety resembles that of *P. pubescens* Loisel. It is dense and canescent. Its leaves have remote and prominent teeth. These differences are distinct enough to warrant it at least a varietal status.

Section 4. *Stenostigma* Koehne

Philadelphus subg. II. *Euphiladelphus* sect. 4. *Stenostigma* Koehne, emend.

Philadelphus Reihe 1. *Corticatae* Koehne, Deutsche Dendr. 179, 180, 1893.

Philadelphus Reihe 3. *Decorticatae racemosae* Koehne, op. cit. 180, 182.

Philadelphus sect. *Stenostigma* Koehne in Gartenfl. 45: 450. 1896; et in Mitt.

Deutsch. Dendr. Ges. 1904(13): 77, 81. 1904, pro parte. — Engler, Pflanzenf. ed. 2, 18a: 193. 1930, pro parte.

Philadelphus Coronarii Rydb. in N. Am. Fl. 22: 162. 1905, in clavi, s. stat.

TYPE SPECIES: *P. coronarius* Linn.

Erect shrubs with rather stiff branchlets, the bark exfoliating or closed; leaves ovate, dentate, rarely semi-entire; flowers in determinate racemes; sepals ovate; petals oblong, ovate or suborbicular; stamens 25 up to 38, rarely over 40; ovary with medianly attached placentas, the style usually divided above, the stigmas clavate, rarely spatulate or oar-shaped; capsules ellipsoid with subapical persistent sepals; seeds usually short-tailed, the lobes on the crown rounded (except some Himalayan and American species).

Geographically, this section has the widest range. Its species occur in every continent of the Northern Hemisphere. From the Ozark Plateau region northwestward to northwestern United States and the adjacent territory of Canada, and from the higher altitudes of northeastern Asia to Japan, Korea, China, the western Himalayan region, the Caucasus and southern Europe, its distribution forms a slightly discontinuous belt girdling the world. Morphologically, several of its very widely separated species such as *P. coronarius* of Europe, *P. triflorus* of the western Himalayan region, *P. tenuifolius* of northeastern Asia, *P. satsumi* of Japan and *P. lewisii* of northwestern United States are hard to distinguish. This is also true with *P. caucasicus* of the Caucasus, *P. subcanus* of Central China, *P. schrenkii* of northeastern Asia, *P. skikokianus* of Japan, and *P. gattingeri* of southeastern United States. The subdivisions of this section are here made more on the basis of geographical separations and less on morphological distinctions of the included species. They are series *Coronarii* of Europe and the Caucasus, *Tomentosi* of western Himalaya, *Delavayani* of southwestern China, *Sericanthi* of China and Korea, *Pekinenses* of north China, *Satsumani* of Japan, *Gordoniani* of northwestern United States, and *Pubescentes* of the interior low plateaus and the Ozark Plateau regions of the United States.

KEY TO THE SERIES

- A. Hypanthia glabrous or rarely with a few hairs at the base.
- B. Adaxial stigmatic surface longer than the abaxial.
 - C. Seeds long-caudate, the embryos half as long as the tails (except *P. triflorus*).
 - D. Leaves glabrous or glabrescent; American species. Ser. 1. *GORDONIANI*.
 - DD. Leaves tomentose beneath; Himalayan species. Ser. 2. *TOMENTOSI*.
 - CC. Seeds medium- or short-caudate, the embryos equal to or longer than the tails.
 - D. Seeds short-caudate, the embryo longer than the tail (except *P. brachibotrys*); northern and eastern Chinese species. Ser. 3. *PEKINENSES*.

DD. Seeds medium-caudate, the embryos equal to the tail; European and Caucasian species. Ser. 4. **CORONARI**.

BB. Adaxial stigmatic surface shorter than the abaxial; southwestern Chinese species Ser. 5. **DELAVAYANI**.

AA. Hypanthia uniformly and, in general, thickly pubescent.

 B. Large shrubs up to 4 or 5 m. high; the lower surfaces of the leaves, the hypanthia and sepals uniformly long villose; southeastern United States species. Ser. 6. **PUBESCENTES**.

 BB. Medium or low shrub, 1-3 m. high; the lower surfaces of the leaves, the hypanthia and sepals strigose or scabrid (except *P. mitsai* from northwest China).

 C. Seeds short-caudate; hair on the hypanthia strigose, scabrid or villose; Chinese species. Ser. 7. **SERICANTHI**.

 CC. Seeds long- or medium-caudate; hair on the hypanthia weak, short, golden, curly, only along the angles or very sparsely all over; Japanese species. Ser. 8. **SATSUMANI**.

Series 1. **Gordoniani** (Koehne) Rehder

Philadelphus subg. II. **Euphiladelphus** sect. 4. **Stenostigma** ser. 1. **Gordoniani** (Koehne) Rehder, Man. Cult. Trees Shrubs ed. 2, 266. 1940; et Bibl. Cult. Trees Shrubs 191. 1949.

Philadelphus sect. *Stenostigma* subsect. *Gordoniani* Koehne in Gartenfl. 45: 450. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904(13): 77, 81. 1904, pro parte. — Engler, Pflanzenf. ed. 2, 18a: 193. 1930.

Philadelphus Coronarii Rydb. in N. Am. Fl. 22: 162. 1905, in clavi, s. stat., pro parte, non Koehne 1896.

TYPE SPECIES: *P. lewisii* Pursh.

Large erect shrubs with brown or gray branchlets, the bark of the second year's growth generally closed; leaves denticulate or subentire; flowers with more or less glabrous hypanthia, the corolla usually cruciform; capsules ellipsoid with super medianly attached persistent sepals; seeds long-caudate. Four species, three in northwestern United States and adjacent Canada, and one in southern United States. Their distribution is shown in map 4.

KEY TO THE SPECIES

A. Petals glabrous.

 B. Disc glabrous.

 C. Anthers glabrous.

 D. Bark of the second year's growth ochraceous, brown or castaneous; western species. 17. *P. lewisii*.

 DD. Bark of the second year's growth cinereous; southeastern species. 18. *P. intectus*.

 CC. Anthers hirtellous 19. *P. trichothecus*.

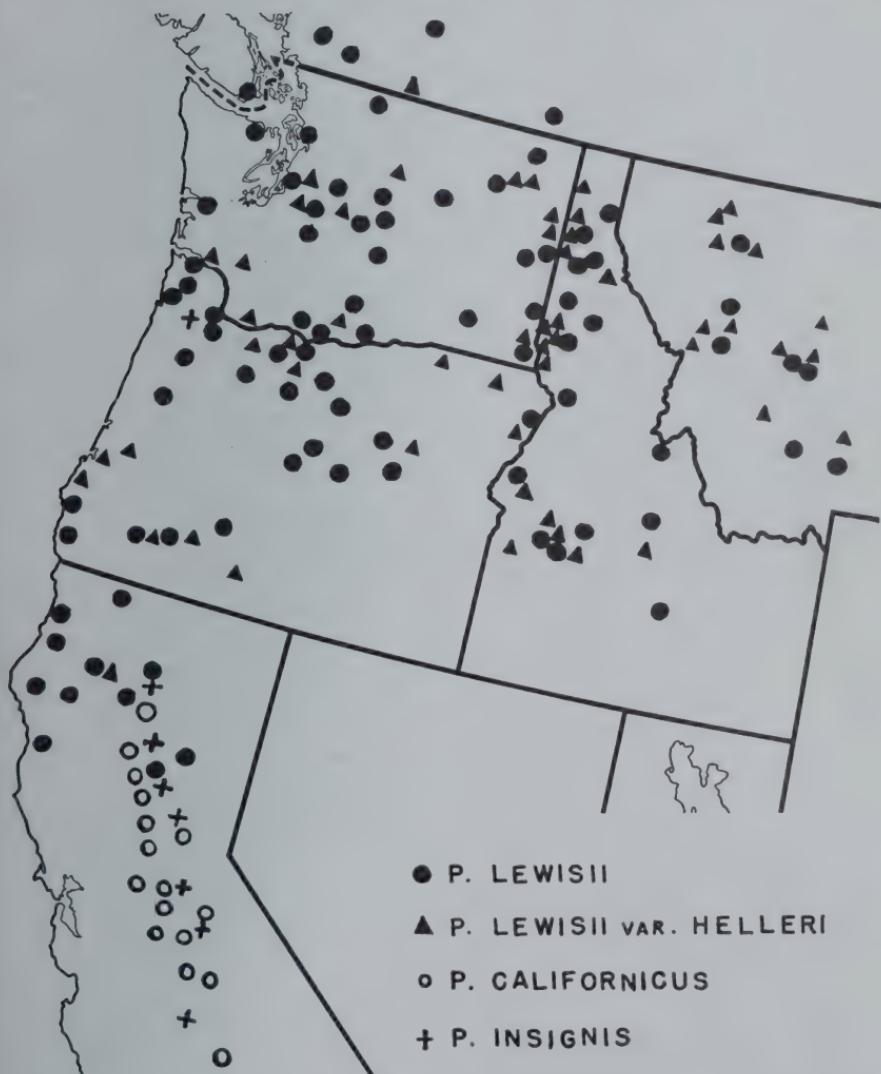
 BB. Disc pilose.

 C. Anthers glabrous; style glabrous, rim of the disk white setose. 20. *P. oreganus*.

 CC. Anthers hirtellous; style and disk pilose. 21. *P. confusus*.

AA. Petals hirtellous on both surfaces. 22. *P. zelleri*.

17. *Philadelphus lewisii* Pursh, Fl. Am. Sept. 1: 329. 1814.—DC., Prodr. 3: 206. 1828.—Schrader in Linnaea 12: 401. 1838.—Hooker, Fl. Bor. Am. 1: 220. 1834.—Torr. & Gray, Fl. N. Am. 1: 595. 1840.—Koch in Woch. Gärtn. Pflanzenk. 2: 229. 1859.—Gray in Bot. Calif. 1: 202. 1876.—Dippel, Handb. Laubh. 3: 344, fig. 181. 1893.—Nicholson, Kew Hand-list 1: 227. 1894, ed. 2. 377. 1902.—Koehne, Deutsche Dendr. 180. 1893; in Gartenfl. 45: 541. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 81. 1904.—Schneider, Ill. Handb. Laubh. 1: 368, fig. 237, s-u. 1905.—Rydb.



MAP 4. The distribution of the species of *Philadelphus* in western United States.

in N. Am. Fl. 22: 165. 1905.—Howell, Fl. Northw. Am. 206. 1898.—Rehder, Man. Cult. Trees Shrubs 272. 1927, ed. 2, 266. 1940; et Bibl. Cult. Trees Shrubs 191. 1949.—Abrams, Ill. Fl. Pac. St. 2: 384, fig. 2304. 1944.—Bean, Trees Shrubs, ed. 7, 2: 636. 1950; et in Chitt. Dict. Gard. 3: 1546. 1951.

Philadelphus globosus hort. ex Koch, Dendr. 344. 1869.

Philadelphus thrysiflorus Hort. ex Nicholson, Kew Hand-list 1: 227. 1894; ed. 2, 377. 1902, in syn.

Philadelphus coronarius nivalis Hort. ex Nicholson, Kew Hand-list 227. 1894; ed. 2, 377. 1902, in syn.

Philadelphus nivalis Hort. ex Nicholson, ll.cc., in syn. non Jacques, 1841.

An erect shrub up to 3 m. high, the branchlets rather stiff, the second year's growth brown, rarely ochraceous or castaneous, the bark closed, with transverse cracks, slowing wearing off; current year's growth glabrous, ciliate at the nodes, buds enclosed. Leaves ovate, 4–5.5 cm. long, 2–3.5 cm. wide, rounded at the base, acute, rarely obtuse or short-acuminate at the apex, semi-entire or inconspicuously denticulate, sparsely strigose-villoso on the nerves above, barbate in the nerve angles and strigose-villoso on the nerves beneath, ciliate on the margins. Inflorescences 7-, 9-, or 11-flowered, rarely on weak branchlets 5-flowered, or flowers ternate or solitary, the rachis sparsely pilose or glabrescent; pedicels 2–7 mm. long, sparsely pilose, the lower ones always in the axils of normal leaves; hypanthia campanulate, glabrous; sepals ovate, 5–6 mm. long, 3 mm. wide at the base, the apex acute or acuminate; corolla cruciform, 3–4.5 cm. across, the petals oblong, 13–22 mm. long, 6–10 mm. wide, the apex rounded and emarginate; stamens 28 up to 35, the longest about half the length of the petals, the anthers oblong, glabrous; disc glabrous, the style shorter than the longer stamens, glabrous, undivided or slightly divided above, the abaxial stigmatic surface 0.5–1.8 mm. long, the adaxial surface twice as long or even longer. Capsules ellipsoid, 7–10 mm. long, 4–5 mm. in diameter, pointed at both ends, the persistent calyx super-median. Seeds long-caudate, the embryo cylindrical, 0.75 mm. long, the tail equal or twice as long, the crown with pointed lobes.

CANADA: British Columbia: Vancouver Island, Victoria, *W. R. Carter*, July 7, 1917 (G), Aug. 21, 1917 (G); *J. Macoun*, July 2, 1887 (MO, NY), Aug. 31, 1877 (NY); *C. F. Newcomer*, Aug. 14, 1916 (G), 328 (F); Fraser Valley, *Fletcher*, June 1885 (G); Sproat, Columbia River, *J. Macoun*, June 27, 1890 (US); *Salmo*, *F. A. MacFadden* 13915 (NY); Chilliwack Valley, *J. Macoun*, Aug. 16, 1901 (G, NY); Lake Osoyoos, *J. Macoun*, June 3, 1905 (F, NY).

UNITED STATES: Washington: Asotin Co., *C. E. Skinner* 116 (F); Chelan Co., Leavenworth, *I. C. Otis* 955 (US), *J. W. Thompson* 6734 (G), *L. M. Umbach* 482 (NY); Lake Chelan, *M. Kelly* 4 (MO); Douglas Co., Grand Coulee, *E. Mackay* 17 (G, MO, NY, US); Moses Coulee, *W. C. & M. W. Muenscher* 11253 (CU); Ferry Co., Colville Nat. Forest, *W. W. Eggleston* 10614 (US); King Co., Seattle, *L. Benson* 1154 (US), *G. Engelmann & C. S. Sargent*, July 18,

1880 (A), *W. J. Eyerdam* (F), *J. G. Jack*, Aug. 18, 1904 (A), *S. M. Zeller*, Aug. 8, 1910 (MO); Kittitas Co., Rock Island, *J. H. Sandberg & J. B. Leiberg* 452 (G, NY, US); Klickitat Co., *W. N. Suksdorf* 1740 (A), 6921 (A), 7011 (A); Mt. Constitution, *H. C. Cowles* 382 (F); Olga, *C. C. Engberg*, June 19, 1905 (NY); Pierce Co., *Wiegand, Castle, Dann & Douglas* 1119 (F); San Juan Island, *C. A. Reynold* 28 (F); Spokane Co., Clark Springs, *F. O. Kreager* 598 (G, NY, US); Spangle, *W. N. Suksdorf* 300 (G); Trout Lake, Mount Rainier Forest Reserve, *J. B. Flett*, July 27, 1899 (US); Walla Walla Co., Blue Mts., *C. V. Piper*, Aug. 2, 1892 (G); same locality, *C. S. Sargent*, Aug. 1, 1896 (A); Walla Walla, *C. L. Shear* 5605 (US); Whatcom Co., *W. C. Muenscher* 7956 (G, CU); Whitman Co., Palouse, *J. G. Jack* 1294 (A); Yakima, *T. S. Brandegee* (A); same locality, *D. Griffiths & J. S. Cotton* 43 (NY, US). Oregon: Lewis River, *Lewis* (fragment of TYPE, NY); Benton Co., Brook Lane, *H. M. Gilkey*, June 16, 1943 (G); Clackamas Co., Milwaukie, *W. N. Suksdorf* 940 (A); Columbia Co., Goble, bank of Columbia River, *A. Rehder*, Aug. 22, 1904 (A); Cow Canyon Co., Madras, *M. E. Peck* 15773 (MO); Crook Co., *F. V. Coville & E. I. Applegate* 712 (A, US); same county, without precise locality, *Herb. Iowa State College* no. 268 (G, MO); Farewell Bend, *J. B. Leiberg* 475 (A, F, G, NY, US); Crook River, *K. Whited* 208a (A); Curry Co., *M. E. Peck* 8829 (BH, G, MO); Dalles of the Columbia River, *G. Engelmann & C. S. Sargent*, Aug. 25, 1880 (A); The Dalles, *J. W. Thompson* 2822 (MO); Farmington, *J. E. Kirkwood* 203 (NY); Forest Grove, *F. E. Lloyd*, Oct. 1849 (NY); Fort Colville to Rocky Mts., *Dr. Lyall* (G); Grant Co., Canon City, *H. E. Brown* 83 (A, MO, NY, US); Grant's Pass, *H. S. Prescott*, May 15, 1912 (G), June 8, 1912 (F); Hood River Co., *L. F. Henderson* 9207 (G, MO); E. Independence, *J. C. Nelson* 1562 (G); Jackson Co., *E. I. Applegate* 2195 (US); Josephine Co., *W. H. Camp* 49 (NY); Klamath Co., Keno, *M. E. Peck* 9418 (G, NY); Multnomah Co., Bridal Veil, *H. H. Smith* 3111 (F); Mount Hood, *H. D. Langille* in 1898 (US); Portland, *E. P. Sheldon* 12087 (F); same locality, *M. W. Gorman* 412 (US), *J. W. Thompson* 845 (MO), *L. S. Rose* 37434 (MO); Sauvie's Island, *H. F. Munroe*, June 1875 (F); Shemman Co., John Day Valley, *L. F. Henderson* 5405 (G, MO); Trail Creek Cañon, *E. P. Sheldon* 8207 (A, G, MO, NY, US); Union Co., *W. C. Cusick*, June-July 1876 (G); *J. W. Thompson* 4847 (MO); Wallowa Co., Wallowa, *M. E. Peck* 18420 (NY); Wallowa Lake, *L. Constance & C. J. Jacobs* 1416 (MO); Snake River Canyon, *Constance, Rollins, & Dillon* 1570 (G); Imnaha, *W. C. & M. W. Muenscher* 15860 (CU); Wasco Co., Hood River, *A. A. Heller* 10098 (A, G, MO, US), *E. P. Sheldon* S 12173 (F); N. W. Wheeler Co., Pine Creek, *M. E. Peck* 10051 (A, NY); without precise localities, *E. Hall* 167 (G, MO, NY), *T. J. Howell* (F), *R. D. Nevins* in 1873 (G). California: Del Norte Co., *Ruth & B. C. Maguire* 15162 (CU); Humboldt Co., Yager Road, *S. K. Harris* 3529 (G), 3530 (G); Plumas Co., *A. A. Heller* 15130 (US); Siskiyou Co., *E. E. Stanford* 1601 (MO); Trinity Co., Weaverville, *J. P. Harrington* (US); *C. Epling & W. Robison*, June 20, 1935 (MO); Yreka, *E. L. Greene*, June 24, 1876 (F, MO); without precise localities, *J. M. Bigelow* in Whipple's Exploration for a Railway Route in 1853-4 (US), *A. Kellogg & W. G. W. Harford* 247 (G, NY, US). Idaho: Boise Co., Boise, *J. A. Clark* 72 (BH, G, US), 319 (BH, G); same locality, *T. E. Wilcox* in June 1881 (G), *C. L. Hitchcock & C. V. Muhlick* 9759; Sweet, *J. F. Macbride* 1623 (F, G, MO, NY, US); Custer Co., Bear Creek, *J. F. Macbride & E. B. Payson* 3369 (G); Lake Coeur d'Alene, *Ruth & B. C. Maguire*, June 12, 1934 (CU); Pend d'Oreille, *E. L. Greene*, Aug. 8, 1889; Coeur d'Alene Mts., Carbon, *J. B. Leiberg* 1515 (US); Kootenai Co., Hope, *A. A.*

Heller 253 (F); same locality, *E. A. Mearns*, June 13, 1903 (US), *J. B. Leiberg*, July 1890 (F), July 1892 (F), *J. H. Sandberg*, July 1888 (US); *Latah Co.*, *Cedar Mt.*, *C. V. Piper*, July 19, 1901 (G); *Clearwater River*, *C. English Jr.* (BH); *Viola*, *D. E. Elmer* 79 (NY, US); *Lemhi Co.*, *Salmon*, *E. B. & L. B. Payson* 1869 (BH, G, MO, NY); *Nez Perces Co.*, *Hatwai Creek*, *Sandberg*, *MacDougal & Heller* 253 (CU, G, NY, US); *Clearwater River*, *F. G. Meyer* 879 (G); *Washington Co.*, *M. E. Jones* 6305 (MO); without precise locality, *T. E. Wilcox* in 1883 (US). *Montana*: *Flathead Co.*, *Big Fork*, *B. T. Butler* 2117 (NY), 2294 (NY); same locality, *L. M. Umbach*, Aug. 11, 1901 (NY); *Galatin Cañon*, *J. W. Blankinship* 172 (F, US); *Glacier National Park*, *B. Maguire & G. Piranian* 15529 (G); *Helena*, *F. D. Kelsey*, June 20, 1887 (F), June 1890 (F), July 7, 1891 (F, G); *Kalispell*, *S. D. McKelvey*, Sept. 18, 1921 (A); *Lake McDonald*, *H. M. Evans*, July 16, 1924 (F); *Madison Co.*, *Pony*, *P. A. Rydberg & E. A. Bessey* 4317 (F, G, NY, US); *Missoula*, *J. E. Kirkwood* 1151 (F, G); *Bridger Mts.*, *W. W. Jones*, July 1905 (G); *Ravalle*, *C. Riss*, June 17, 1888 (A); *Swan Lake*, *H. N. Whitford* 18 (F); *Sixteen Mile Creek*, *W. M. Canby* 52b (US); without precise locality, *W. J. Howard* s.n. (G).

CULTIVATED: *Europe*: *Kew*, A. 19, *Macklearn* 429 (BH); *Hort. Bot. Berol.*, *E. Koehne* 218 (G); *Hort. Götting.*, *A. Rehder* 1654 (A); *Plantières*, *C. Schneider*, Sept. 1903 (A). *United States*: *Arnold Arboretum* 543-4 = 5876 (A), 543-5 = 15370 (A), 1004-30 (A).

This species was described on the basis of Lewis' collection made "on the Waters of Clark's River." This locality was interpreted by Piper¹ as the "Hellgate River, between Missoula, Mont., and the mouth of Big Blackfoot River, in Missoula county, Montana," and by Rydberg² as the "Clark's Fork of Columbia River in Montana." The label which accompanied the fragment of the type in the New York Botanical Garden gives the type locality as "Oregon, Lewis River."

Since the publication of *P. lewisii* Pursh, several binomials have been established on the strength of the pubescence of the leaves, the color of the bark of the stem, the degree of division of the style, or the shape of the apex of the sepals. The large amount of material that I have examined clearly demonstrates that none of these characters is constant and that they are unreliable for distinguishing species. The type of *P. lewisii* Pursh is a fruiting specimen. Its leaves are rather small, 2.5-4 × 1.3-2.2 cm., acute at the apex, sparsely pubescent above, and also on the nerves and in the nerve angles beneath. The apices of the persistent sepals on the fruit are acute. A large number of the specimens that match with the type in these respects have oblong petals and cruciform corollas. This character is also interpreted as typical of *P. lewisii* Pursh in this study. Specimens with obovate petals and disciform corollas are considered as a variety of *P. lewisii* Pursh. The wild populations of this species do exhibit definite patterns in the size and form of the leaves. These are treated as different forms of the typical *P. lewisii* Pursh.

Philadelphus lewisii has a wide range, from British Columbia down the Pacific coastal states to California and eastward to Montana and Idaho.

¹ C. V. PIPER, New and noteworthy plants, in Bull. Torrey Bot. Club 29: 226. 1902.

² P. A. RYDBERG, Hydrangeaceae, in North American Flora 22: 165. 1902.

In this large area it tolerates greatly varied ecological conditions. In Victoria it grows in lowland woods. In Washington it has been collected in the rocky draws among the sagebrushes. In Oregon it is found to be common in thickets, on the banks of rivers, on bluffs and in canyons. It has also been observed to grow in grassy openings associated with *Berberis* and *Quercus* in the cutover *Pseudotsuga* groves. In Idaho it occurs on cliffs and rock slides at altitudes of 900–1830 meters. Normally it grows from two up to three meters high, and its white, slightly fragrant flowers appear from late May to early July.

Although *Philadelphus lewisii* is a native of the United States, when compared with the other species cultivated in the American gardens, it is a very rare plant in this country. So far as I know, the few specimens existing in the outstanding American arboreta and botanical gardens are imported, with only one exception, from European nurseries. For example, Arnold Arboretum 5876 was imported in 1909 from the Späth nursery, and 543-5 was from Simon Louis nursery. In 1930 E. J. Palmer moved a living plant from Wolf Creek of Montana to the Arnold Arboretum (1004-30). It flowered in 1936, but has not done well in New England.

KEY TO THE VARIETIES OF *P. lewisii*

- A. Hypanthia completely glabrous.
- B. Base of the leaf rounded; lamina ovate or oblong, 2–5 cm. wide (except var. *parvifolius*).
 - C. Leaves subcoriaceous, those on the flowering branches subentire or inconspicuously denticulate, the length equal to or longer than twice the width.
 - D. Petals obovate, the corolla disciform; leaves ovate or oblong-ovate.
 - E. Leaves on the flowering branches 4–6 cm. long.
 - EE. Leaves on the flowering branches 1–2 cm. long.
 - DD. Petals oblong, the corolla cruciform; leaves oblong.
 - c. var. *oblongifolius*.
 - CC. Leaves chartaceous, suborbicular or broad ovate, those on the flowering shoot usually dentate or serrate, the length less than twice the width.
 - d. var. *platyphyllus*.
 - BB. Base of the leaf acute; lamina lanceolate, 6–14 mm. wide.
 - e. var. *angustifolius*.
 - AA. Hypanthia with few hairs.
 - B. Leaves ovate or oblong, the base rounded.
 - C. Lamina 3–8 cm. long.
 - f. var. *helleri*.
 - CC. Lamina 1.5–2.5 cm. long.
 - g. var. *intermedius*.
 - BB. Leaves elliptic, the base acute or obtuse.
 - h. var. *ellipticus*.

17a. *Philadelphus lewisii* var. *gordonianus* (Lindl.) Jepson, Man. Fl. Pl. Calif. 466. 1925.—McMinn, Ill. Man. Cal. Shrubs 139, fig. 136. 1939.

Philadelphus gordonianus Lindl. in Bot. Reg. 24 (Misc. Not.): 21. 1838; 25: pl. 32. 1839.—Torr. & Gray, Fl. N. Am. 1: 595. 1840.—Walp., Repert. 2: 151. 1843.—Gray, Bot. Calif. 1: 202. 1849.—Decaisne & Naudin, Man. Amat. Jard. 3: 69, fig. 19. 1868.—Lavallée, Arb. Segrez. Enum. 116. 1877.—Nicholson, Ill. Dict. Gard. 3: 95, fig. 7. 1886.—Rattan, Pop. Cal. Fl. 57. 1879, ed. 8, rev. 57. 1892.—Dippel, Handb. Laubh. 3: 342. 1893.—Koehne in Gartenfl. 45: 542. 1896.—Rydb. in N. Am. Fl. 22: 167. 1905.—Gordon in Jour. Roy. Hort. Soc. London 34: 12, fig. 6. 1908.—Mottet, Arbres Arb. Orn. Pleine Terre 224. 1925.—Rehder, Man. Cult. Trees Shrubs 272. 1927, ed. 2, 267. 1940; et Bibl. Cult. Trees Shrubs 191. 1949.—Gilkey, Handb. Northw. Fl. Pl. 147, fig. [1]. 1942.—Abrams, Ill. Fl. Pac. St. 2: 384, fig. 2303. 1944.—Bean, Trees Shrubs ed. 7, 2: 413. 1950; et in Chitt., Dict. Gard. 3: 1546. 1951.

Philadelphus cordatus Petzold & Kirchner, Arb. Muscav. 203. 1864.

Philadelphus grahami Petzold & Kirchner, l.c.

Philadelphus californicus sensu Carrière in Rev. Hort. 1866: 339. 1866, non Benth.

Philadelphus lewisii sensu Piper in Bull. Torr. Bot. Club 29: 225. 1902, non Pursh.

Philadelphus gordonianus var. *columbianus* (Koehne) Rehder in Jour. Arnold Arb. 1: 196. 1919; Man. Cult. Trees Shrubs 272. 1927, ed. 2, 267. 1940; et Bibl. Cult. Trees Shrubs 191. 1949.

Philadelphus columbianus Koehne in Gartenfl. 44: 542. 1896.—Rydb. in N. Am. Fl. 22: 166. 1905.—Schneider, Ill. Handb. Laubh. 1: 368, fig. 236, k. 1905.

TYPE: Cult. London Hort. Soc., July 9, 1838 (ISOTYPE, G).

An erect shrub; the leaves ovate, those of the vegetative shoots 5–6 cm. long, 2.5–4 cm. wide, uniformly sparsely pubescent beneath, glabrous and inconspicuously pilose along the nerves above, coarsely dentate, each side with 4 or 5 large outward pointing teeth in the middle, rounded at the base, shortly acuminate at the apex; the leaves on the flowering branch ovate, 3–5 cm. long, 1.5–3.5 cm. wide, subentire or minutely serrulate, glabrous on both surfaces, except the nerves inconspicuously pilose; hypanthia and sepals glabrous; corolla disciform, 3.5–4.5 cm. across, the petals obovate, 1.5–2 cm. long, 1.2–1.9 cm. wide, rounded at the apex; stamens ca. 35; capsules ellipsoid, 10 mm. long, 4 mm. in diameter.

UNITED STATES: Washington: W. Klickitat Co., W. N. Suksdorf, June 14, 1881 (US); Walla Walla Co., L. O. Anderson, June 8, 1883 (BH). Oregon: Curry Co., Rogue River near Elk Creek, J. B. Leiberg 4181 (US); Crook Co., Blue Mountains, W. W. Eggleston 11378 (US); Wallowa Co., near Wallowa, A. W. Sampson & G. A. Pearson 79 (US); without precise locality, T. J. Howell, July 1880 (US). California: Mendocino Co., Round Valley, V. K. Chestnut 119 (US). Montana: Big Fork, B. T. Butler 2117 (NY).

CULTIVATED: Europe: London Hort. Soc., Lindley, July 9, 1838 (G, specimen from the TYPE plant); Hort. Bot. Berl., E. Koehne 9 (ISOTYPE of *P. columbianus* Koehne, G); Hannover, Bot. Gart. Forstakadamie, H. Zabel 2 (BH), 13 (BH); Breslau, C. Baenitz, July 4, 1899 (A), June 27, 1907 (A, BH). Canada: Ottawa, Dominion Arboretum 97–485–1, M. N. Zinch 1566 (BH).

United States: Arnold Arboretum 4619 = 2221-4, A. Rehder, June 24, 1909 (A). New York, Rochester, Highland Park, Mrs. R. E. Horsey, Sept. 21, 1917 (BH), June 16, 1918 (BH).

Philadelphus gordonianus Lindl. was described on the basis of a living specimen raised from the seed sent to London by Douglas. A specimen collected from the type plant on July 9, 1838, is preserved in excellent condition in the Gray Herbarium. The leaves on the vegetative shoots of this specimen are pubescent and coarsely dentate. Those on the flowering shoot are subentire and glabrous. In the indumentum on the leaf-surfaces and the dentation along the margin this specimen does not differ from the typical *P. lewisii* Pursh. Nevertheless, the petals of its large flowers are broad obovate and the corolla more or less disciform. This specimen and the spontaneous material that matches with it in the disciform corolla are treated as a variety of *P. lewisii* Pursh, a species characterized by cruciform flowers. In this variety there is a considerable variation in the color of the bark of the second year's growth. The bark of the type plant is castaneous and tardily exfoliate, that of the Oregon and Montana material is reddish brown and closed, and that of the specimens from Washington and California is gray and closed. Judging from the material I have examined, this variety is very rare in American gardens.

17b. *Philadelphus lewisii* var. *parvifolius*, var. nov.

Frutex parvus, ramis cinereis, bienniis castaneis, 2-3 mm. diametro, transverse rimulosis, hornotinis glabris, ad nodos ciliatis; foliis parvis, ovatis vel oblongo-ovatis, 1-2 cm. longis, 5-8 mm. latis, utrinque obtusis, raro basi rotundatis, integerrimis ciliatisque, supra glabris vel sparse pilosis, subtus glabris et in axillis nervorum barbatis; inflorescentiis 3- vel 5- raro 1-floris, rhachibus 5-10 mm. longis, pedicellis pilosis, hypanthiis glabris; sepalis ovatis, acutis; corolla disciformi, 1.5-2 mm. diametro, petalis oblongo-ovatis, 7-10 mm. longis, 5-8 mm. latis, apice rotundatis, staminibus ca. 30; disco glabro, stylo 5 mm. longo, $\frac{1}{3}$ - $\frac{1}{2}$ diviso, stigmatibus clavatis; capsulis ignotis.

UNITED STATES: Montana: Missoula, J. E. Kirkwood 1151 (TYPE, F; fragment A; MO, ISOTYPE); Helena, B. T. Butler 865 (NY).

This variety is distinguished by its small habit, entire, oblong-ovate leaves and small, very much crowded flowers. In appearance it reminds one of the hybrid *P. lemoinei*, but this hybrid and its various forms all have pubescent, broad-ovate, serrate, or elliptic-lanceolate leaves. The type of this variety was collected in the prairie of Missoula. Mr. M. Canoso of the Gray Herbarium knows that country well, and he assures me that it is a spontaneous plant. Doubtlessly it is closely related to Nelson's *P. intermedius*, but the original description of the latter calls for broad-ovate, short-petiolate, or subsessile leaves and "foliose-bracted" flowers. Nelson cited no specimens. My material which fits his description has sparsely puberulous hypanthia.

17c. *Philadelphus lewisii* var. *oblongifolius*, var. nov.

A typo recedit foliis oblongis vel oblongo-ellipticis, 4–6.5 cm. longis, 1.3–3 cm. latis, utrinque obtusis vel interdum apice acutis, integris vel raro inconspicuis crenatis; hypanthiis glabris, sepalis ovato-lanceolatis; corolla disciformi, 3–4 cm. diametro, petalis oblongis, 1.5–2 cm. longis, 1 cm. latis, apice erosis, subrotundatis; disco et stylo glabris.

UNITED STATES: Washington: Chelan Co., Wenatchee, *K. Whited* 143 (US), 1175 (US); Whitman Co., Wawawai, *C. V. Piper* 3838 (G, NY; US, TYPE); Seattle, *C. A. Mosier* (US); Yakima region, North Fork, *J. Cotton* 465 (US); Rattlesnake Mountain, *J. Cotton* 674 (G, US). Oregon: Jackson Co., Wimer, *E. W. Hammond* 123 (US). California: Humboldt Co., Valley of the Van Duzen River, *J. P. Tracy* 2886 (US); Hupa Indian Reservation, *H. P. Chandler* 1333 (G, NY, US).

This variety is distinguished from the typical *P. lewisii* by its oblong or oblong-elliptic leaves with obtuse bases. Its flowers are large, and its introduction into cultivation is desirable.

17d. *Philadelphus lewisii* var. *platyphyllus* (Rydb.), comb. nov.

Philadelphus platyphyllus Rydb. in N. Am. Fl. 22: 167. 1905.

Philadelphus gordonianus sensu Abrams, Ill. Fl. Pax. St. 2: 384. 1944, pro parte, non Lindl.

TYPE: California, Mt. Shasta, *H. E. Brown* 562 (NY).

Bark of the second year's growth gray, closed, the current year's growth glabrous; leaves broad elliptic or suborbicular, rarely ovate, 4.5–7 cm. long, 2.5–5 cm. wide, rounded at the base, acute at the apex, coarsely dentate or subentire, glabrous or rarely sparsely pilose above, bearded and more or less glabrous beneath; inflorescences 5-, 7-, or 9-flowered, the lower pairs in the axils of normal leaves; pedicels, hypanthium and calyx glabrous, the sepals ovate-elliptic, 6 mm. long, 3 mm. wide; corolla cruciform, 3.7–4.5 cm. across, the petals oblong-ovate, rounded at the apex; stamens ca. 38, the longest 7–9 mm. long; disc and style glabrous, the latter 4 mm. long, the stigma oar-shaped.

UNITED STATES: Washington: Cape Horn, *C. V. Piper* 5031 (G, US); Klickitat Co., *W. N. Suksdorf* 6641 (NY), 6922 (NY). California: Siskiyou Co., south side of Mt. Shasta, *H. E. Brown* 562 (NY, TYPE; US, ISOTYPE); Trinity Co., *W. H. Brewer*, 1864 (US); without precise locality, *A. Kellogg & W. G. W. Harford* 247 (NY). Idaho: without precise locality, *F. V. Coville & T. H. Kearney Jr.* 234 (US). Montana: Big Fork, *B. T. Butler* 547 (NY).

This variety can be distinguished from the typical *P. lewisii* Pursh and other related forms by its large, broad-elliptic or suborbicular, chartaceous leaves. Rydberg considered it a species. As there is no essential difference between this taxon and *P. lewisii* Pursh other than the texture and general appearance of the leaves, I think it warrants no higher rank than a variety.

Rydberg recorded the type as *Brown* 561. But the type material de-

posed in the New York Botanical Garden, as well as the isotypes in the United States National Herbarium, all have the number 562 on the labels. This discrepancy is apparently a clerical error.

17e. *Philadelphus lewisii* var. *angustifolius* (Rydb.), comb. nov.

Philadelphus angustifolius Rydb. in N. Am. Fl. 22: 166. 1905.

Philadelphus gordonianus sensu Abrams, Ill. Fl. Pac. St. 2: 384. 1944, pro parte, non Lindl.

TYPE: Washington, *Mrs. Bailey Willis*, in 1883 (NY).

Bark of the second year's growth castaneous, exfoliate or tardily exfoliate, the current year's growth sparsely pilose; leaves lanceolate, 3–4.5 cm. long, 6–14 cm. wide, acute at the base, shortly acuminate at the apex, glabrous (except the nerves) on both surfaces, subentire or inconspicuously serrulate with one or two teeth on each side; inflorescences, 5-, 7- or rarely 9-flowered, the lower pairs in the axils of normal leaves; hypanthium and calyx glabrous; corolla cruciform, 3 cm. across, the petals oblong, 1.3 cm. long, 5–7 mm. wide, the apex rounded; disc and style glabrous, the stigma oar-shaped.

UNITED STATES: Washington: Palace Camp, *Mrs. Bailey Willis*, in 1883 (NY, TYPE); Tacoma, *Mrs. Bailey Willis*, in 1883 (NY).

This narrow-leaved variety is known only from the type collection. It is very distinct because of its lanceolate leaves. As the width of the leaves is regarded as an insufficient specific character for the northwestern American *Philadelphus*, this taxon is treated as a variety of *P. lewisii* Pursh.

17f. *Philadelphus lewisii* var. *helleri* (Rydb.), comb. nov.

Philadelphus helleri Rydb. in N. Am. Fl. 22: 166. 1905.

TYPE: Idaho: *A. A. & Gertrude Heller* 3374 (NY).

Bark of the second year's growth brown, castaneous, or cinereous, closed with transverse cracks, the current year's growth sparsely pilose, glabrescent; leaves oblong-ovate or ovate, glabrous or along the nerves or near the base sparsely pilose, 3–6 cm. long, 1.5–2.8 cm. wide, rounded at the base, acute or rarely obtuse at the apex, subentire or inconspicuously serrulate; inflorescences 7- or 9-, rarely 5-flowered, the lowermost pair in the axils of normal leaves; hypanthium and sometimes the calyx sparsely pilose; corolla cruciform, 3–4 cm. across, the petals oblong, the apex obtuse or rounded; disc and style glabrous.

CANADA: British Columbia: Gale, *G. Engelmann & C. S. Sargent*, July 23, 1880 (A); between Cascade and Rossland, *J. W. Thompson* 14415 (A, MO, NY); Oliver, *O. J. Murie* 1189 (MO); Nelson, *J. Fletcher* 621 (MO).

UNITED STATES: Washington: Asotin Co., bank of Snake River, *C. L. Hitchcock et al.* 8367 (BH, G); Chehalis Co., Satsop, *A. A. & G. Heller*

4023 (F, G, US); Chelan Co., *E. A. Purer* 7790 (MO); Cowlitz Co., *F. V. Coville* 703 (US); Ferry Co., Boulder Creek, *W. W. Eggleston* 10621 (US); King Co., Savage, *Cameron & Lenocker*, June-July 1898 (F); *C. A. Mosier*, June 8, 1892 (US); Kittitas Co., *A. D. E. Elmer* 380 (NY, MO, US); Ellensburg, *K. Whited* 518 (US), *J. W. Thompson* 6721 (G, MO); Muckleshute Prairie, *Dr. Ruhn* (F, G); Palouse, *J. G. Jack* 1367 (A, US); Spokane Co., *Dr. Holmes* 966 (NY, US), *J. G. Jack* 1402 (A), 1418 (A), 1457 (A, US), *C. V. Piper* (NY); without precise locality, *G. R. Vasey* 349 (G). Oregon: Columbia River banks, *H. Y. Edward*, July 1873 (NY); Blue Mountain Springs near Prairie City, *M. E. Peck* 10318 (A); Coos Co., *W. Hayon* in 1911 (F); Columbia Co., Goble, *J. G. Jack*, Aug. 22, 1904 (A); Dayville, *W. E. Lawrence* 1014 (US); Hood River, *C. S. Sargent*, Aug. 14, 1896 (A); Jackson Co., *C. L. Hitchcock & J. S. Martin* 4983 (NY), *E. W. Hammond* 123 (MO); Klamath Co., *E. R. Kalmbach* in 1939 (US); Minam River, *E. P. Sheldon* 9047 (A, NY, US); Multnomah Co., *J. Howell*, June 1879 (A); Wallowa Co., Imnaha National Forest, *F. V. Coville* 2416 (US); Imnaha, *M. E. Peck* 17657 (NY); Wallowa Lake, *C. L. Shear* 5612 (US); Wasco Co., Cow Canyon, *F. V. Coville & E. I. Applegate* 675 (US); data on localities not clear, *W. C. Cusick* 106 (F), *J. Howell* in 1880 (US); *J. T. Jardine* 65 (US). California: Along Eel River, *B. Davy & W. C. Blasdale* 5547 (US); without precise locality, *G. R. Vasey* in 1875 (US). Idaho: Boise Co., *Muhlick* 9759 (NY); bank of Boise River, *J. A. Clarke* 319 (F, MO); *C. N. Woods & I. Tidestrom* 2586 (US); Bay Horse, *L. F. Henderson* 3795 (US), *J. S. Newberry*, Aug. 1881 (NY); Canyon Co., Big Willow, *J. F. Macbride* 102 (G, MO, NY, US); Lake Coeur d'Alene, Capse, *G. B. Aiton* 3091 (NY, US); Coeur d'Alene, *H. J. Ruth* 125 (US); Idaho Co., Salmon River, *W. C. & W. W. Muenscher* 15414 (CU); Kootenai Co., St. Maries, *H. D. House* 4927 (US); Latah Co., Moscow, *L. Abrams* 839 (A); *J. G. Jack* 1287 (A), 1289 (A), *M. Murley* 1734 (NY); Nez Perces Co., Lake Waha, *A. A. & G. Heller* 3347 (NY, TYPE; F, MO, ISOTYPES); Hatwai Creek, *Sandberg, MacDougal & Heller* 253 (G, NY, PARATYPES of *P. confusus* *Piper*); Nez Perces Reservation, Lewiston, *A. A. Heller*, May-June 1892 (F); same locality, *L. F. Henderson* in 1894 (US); without precise locality, *J. H. Sandberg*, June 1892 (G, NY); Priest Lake, *D. T. MacDougal* 175 (NY); Shoup, *J. F. Kemp* 65 (NY); Shoshone Co., *E. J. Palmer* 37804 (A, MO); Washington Co., Ruth Creek, *M. E. Jones* 6305 (NY); without precise locality, *G. Ainslie* in 1874 (US). Montana: Bear Gulch, *E. W. Scheuber*, July 17, 1901 (F, NY); Beartown, *E. Scheuber*, July 18, 1901 (NY); Beaverhead Co., Pioneer Range, *C. L. Hitchcock & C. V. Muhlick* 13026 (BH, MO); Flathead Co., Big Fork, *B. T. Butler* 7026 (NY); Columbia Falls, *J. G. Jack* 1575 (A), *S. D. McKelvey*, Sept. 20, 1921 (A); Flathead Lake and vicinity, *Mrs. J. Clemens* (F), *H. T. & J. M. Roger* 1056 (MO, NY); Gallatin Co., Gallatin Cañon, *F. Tweedy* 1261 (NY); Granite Co., *C. L. Hitchcock & C. V. Muhlick* 14414 (MO); Lewis & Clark Co., Wolf Creek, *E. J. Palmer* 36963 (A, MO, NY, US); Lake St. Marz, *S. D. McKelvey*, Sept. 9, 1921 (A); Lost Horse, *J. B. Leiberg* 2918 (US); Missoula Co., Flackfoot, *W. G. Chapman* 26 (NY); Missoula, *C. L. Hitchcock & C. V. Muhlick* 9090 (NY); Head of Jocko River, *C. S. Sargent*, July 15, 1883 (A); The Lo-Lo, *M. J. Elrod* 127 (MO, NY), Lolo National Forest, *E. J. Palmer* 37770 (NY, MO, US); Mission Mts., *D. T. MacDougal* 526 (NY, US); Rival Co., *C. L. Hitchcock & C. V. Muhlick* 14520 (MO); Silver Bow Co., *F. Tweedy* 66 (NY); Swan Lake, *J. G. Jack* 2376 (A); Tenderfoot, *R. S. Williams*, July 31, 1891 (NY).

CULTIVATED: Europe: Hort. Göttingen, A. Rehder 402 (A). Canada: Ottawa, Dominion Arboretum 09-147-2, J. M. Gillett 7131 (A), 7133 (BH). United States: Arnold Arboretum 543, without collector, July 4, 1890 (A), Sept. 19, 1890 (A), June 29, 1910 (A); same stock, W. N. Manning in 1923 (BH); Arnold Arboretum 543-3 = 5876, without collector, June 30, 1913 (A); Arnold Arboretum, E. J. Palmer, June 18, 1936 (A). Washington, D.C., G. R. Vasey, June 4, 1879 (US). Rochester, Highland Park, Mrs. R. E. Horsey, June 17, 1918 (BH), Sept. 4, 1918 (BH).

This variety differs from typical *P. lewisii* Pursh only in the presence of some hairs on the hypanthium and calyx. It is more commonly met with in American gardens than the typical *P. lewisii*. Besides the stocks imported from European nurseries in the late 1800's, it was independently transplanted from California to Washington by Vasey and from Montana to the Arnold Arboretum by Palmer.

17g. *Philadelphus lewisii* var. *intermedius* (Nelson), stat. nov.

Philadelphus intermedius Nelson in Bot. Gaz. 42: 53. 1906.

LECTOTYPE: Idaho, J. F. Macbride & E. B. Payson 3037 (US).

Bark of the second year's growth castaneous, closed, transversely rimulose, tardily wearing off; the current year's growth sparsely weak villose, later glabrescent; leaves broad ovate, 1.5-2.5 (rarely up to 3 cm.) long, 8-15 (rarely up to 22 mm.) wide, rounded at the base, acute or obtuse at the apex, entire or faintly denticulate with one or two teeth on each side, hirtellous on both surfaces or glabrescent; inflorescences 3-, 5-, rarely 7- or 9-flowered, the lower pairs in the axils of normal leaves; hypanthia and sepals sparsely pilose; corolla subdisciform, 2.5 cm. across, the petals ovate, 9-10 mm. long, 7-8 mm. wide, the apex rounded; stamens ca. 35; disc and style glabrous.

UNITED STATES: Oregon: Wallowa Co., Jim Creek, E. P. Sheldon 8283 (A, NY). Idaho: Blaine Co., Martin, J. F. Macbride & E. B. Payson 3037 (US, LECTOTYPE; MO). Montana: Bittiwort Valley, S. Watson 138 (G, US).

When Nelson published *P. intermedius*, he cited no specimen. According to his description his taxon represents a small-leaved form with broadly oval to ovate, shortly petiolate or subsessile leaves rounded at the base, and foliose-bracted flowers. *Macbride & Payson 3037* seems to fit that description best. This collection has sparsely pilose hypanthia and calyces. It is selected to represent the type of this small-leaved pubescent variety.

17h. *Philadelphus lewisii* var. *ellipticus*, var. nov.

Frutex, ramulis brunneis, hornotinis sparse pilosis, glabrescentibus; foliis ellipticis 4-7 cm. longis, 2-3.5 cm. latis, utrinque acutis, raro apice breviter acuminatis, chartaceis, subintegris vel remote inconspicuo-denticulatis, supra glabris raro sparse pilosis, subitus ad nervos strigoso-pilosis, barbatis; inflorescentiis, 5-, 7-, raro 9-floris; hypanthiis sparse pilosis;

sepalis ovatis, 4–6 mm. longis, acutis vel acuminatis; corolla cruciformi, 3.5 cm. diametro, petalis oblongis, 14–16 mm. longis, 7 mm. latis, glabris; staminibus ca. 30, antheris glabris; disco et stylo glabro.

CANADA: British Columbia: Vancouver Island, Saanichton, *I. Mounce*, July 7, 1939 (NY); Victoria, *J. Macoun* 231 (G, NY, US), 86468 (NY).

UNITED STATES: Washington: Chelan Co., Wenatchee Mountains, *J. W. Thompson* (A, G); Klickitat Co., Major Creek, *W. N. Suksdorf* 1741 (A); Spokane Co., N. Spokane, *J. G. Jack* 1456 (A), *F. O. Kreager* 31 (G, NY, US); Wahkiakum Co., Altoona, *W. N. Suksdorf* 6815 (A); Wawawai, Snake River, *E. R. Lake*, July 4, 1892 (F, US). Oregon: Birch Bay, *Dr. Holmes*, in 1838–42 (NY, US); Douglas Co., *L. F. Ward* 56 (NY, US); Grant Co., Grant's Pass, *Munson Hopkins*, Aug. 31, 1889 (US); Jackson Co., Walker Creek, *E. I. Applegate* 2341 (US); Klamath Co., *F. V. Coville* & *E. I. Applegate* 269 (A, TYPE; US, ISOTYPE); Klamath Falls, *E. I. Applegate* 184 (G, US); Spencer Creek, *E. I. Applegate* 2085 (US); Klamath Indian Reservation, *F. V. Coville* 1522 (US); Lake Chalan, *M. W. Gorman* 628 (US); Portland, *F. A. Walpole* 272 (US); Umatilla Co., Pilot Rock, *W. W. Eggleston* 12671 (US). California: Humboldt Co. or Mendocino Co., *H. N. Bolander* (G, US); Laytonville, *A. Eastwood* 9308 (BH); Fieldbrook, *J. P. Tracy* 8646 (A); Trinity Co., *L. Benson* 2194 (MO, NY, US). Idaho: Benton Co., Priest River, *C. C. Epling* 7929 (US); Coeur d'Alene Mountains, Clark's Fork, *J. B. Leiberg* 1666 (US); Nez Perces Co., *W. W. Eggleston* & *H. St. John* 21991 (US). Montana: Columbia Falls, *J. G. Jack* 2419 (A), *R. S. Williams* 678 (US); Flathead Lake, *M. C. Jones* 8370 (US).

18. *Philadelphus inectus* Beadle in Biltm. Bot. Stud. 1: 160. 1902.—Koehne in Mitt. Deutsch. Dendr. Ges. 1904 (13): 82. 1904.—Rydb. in N. Am. Fl. 22: 167. 1905.—Schneider, Ill. Handb. Laubh. 1: 368. 1905.—Beadle in Small, Fl. 507. 1903, ed. 2, 507. 1913; et in Small, Man. South. Fl. 599. 1933.

Philadelphus pubescens var. *inctetus* (Beadle) A. H. Moore in Rhodora 17: 123. 1915.—Rehder, Man. Cult. Trees Shrubs 273. 1927, ed. 2, 267. 1940; et Bibl. Cult. Trees Shrubs 191. 1949.

Philadelphus sanguineus Hort. ex Nicholson, Kew Hand-list ed. 2, 377. 1902, in syn.

TYPE: Tennessee, Nashville, Biltmore Herb. 11378 (photo & fragment A, NY).

An erect tall shrub up to 5 m. high, the branches cinereous, the second year's growth 3–4 mm. in diameter, the bark closed, the current year's growth glabrous, the nodes not ciliate. Leaves ovate or oblong-elliptic, those on the vegetative shoot 6–9.5 cm. long, 4–6 cm. wide, those on the flowering shoot 3–6 cm. long, 1.5–3.5 cm. wide, rounded or obtuse at the base, acuminate at the apex, the acumen 5–10 mm. long, glabrous on both surfaces, remotely and finely serrulate along the apical half of the margin, ciliate; petioles 4–7 mm. long, sparsely ciliate. Inflorescences 5-, 7-, or 9-flowered, the lower pairs in the axils of normal leaves; pedicels 4–6 mm.

long, glabrous; hypanthia campanulate, glabrous; sepals ovate, 6 mm. long, caudate at the apex; corolla disciform, 3 cm. across, the petals oblong-obovate, 15 mm. long, 12 mm. wide, the apex rounded and erose; stamens ca. 38; disc and style glabrous, stigmas spatulate, the adaxial surface three times longer than the abaxial. Capsules subglobose ellipsoid, 5–7 mm. long, 4–5 mm. in diameter, the persistent calyx subapical. Seeds medium- or long-caudate, the embryo 1.25 mm. long, the tail as long or a little shorter.

UNITED STATES: Kentucky: Lyon Co., Kuttawa, *W. W. Eggleston* 4544 (NY). Tennessee: Nashville, Bluff of the Cumberland, Biltmore Herb. 11378 (fragment and photo of TYPE, A, NY), 11378c (TOPOTYPE, NY); same locality, *C. D. Beadle*, June 1899 (A, very likely an ISOTYPE), *T. G. Harbison* 67 (A). Oklahoma: Le Flore Co., Page, *E. J. Palmer* 21623 (A, NY, US).

CULTIVATED: Europe: Villa Thuret, May 30, 1889; Hort. Bot. Berol. 10, *E. Koehne*, June 19, 1894 (G), July 10, 1895 (G), Sept. 3, 1894 (G). United States: Arnold Arboretum 4454, without collector, Sept. 10, 1913 (A); 4454-2, *A. Rehder*, July 18, 1918 (A); 539-6 = 15339, without collector, June 30, 1913 (A), Sept. 10, 1913 (A), same number, *A. Rehder*, July 1, 1916 (A); 15358, *E. J. Palmer*, June 11, 1936 (A), 15376, *C. K. Allen*, June 21, 1927 (A); 1052-36, *E. J. Palmer*, Oct. 3, 1940 (A), June 24, 1943 (A).

Philadelphus inectus Beadle was described on the basis of a specimen collected on the bluffs of the Cumberland River below Nashville. Beadle's detailed description portrays the type exactly. Its completely glabrous leaves and hypanthia suggest a close relationship with *P. lewisii* Pursh. Its stiff upright tall habit and its ovate or oblong-elliptic leaves resemble those of *P. pubescens* Lois. Moore maintained that the differences between *P. pubescens* Lois. and *P. inectus* Beadle are comparable to those between *P. coronarius* Linn. and *P. tomentosus* Wall. As he accepted the combination *P. coronarius* var. *tomentosus* (Wall.) Hook. f. & Thom., he also established the trinomial *P. pubescens* var. *iectus* (Beadle) Moore. Rehder differs from Moore in keeping *P. coronarius* Linn. and *P. tomentosus* Wall. as distinct species but accepted Moore's interpretation of treating *P. inectus* Beadle as a variety of *P. pubescens* Lois. As there is actually a closer tie between *P. inectus* Beadle and *P. lewisii* Pursh than between the former and *P. pubescens* Lois., I can see no justification in keeping it as a variety of the last-named species.

Philadelphus inectus was introduced into cultivation long before it was properly named. Villa Thuret received seeds from C. S. Sargent labeled *P. hirsutus* in the 1880's. In the Botanical Garden of Berlin a plant interpreted by Koehne as *P. gordonianus* was under cultivation before the 1890's. The same taxon was distributed by the Späth and other nurseries as *P. "sanguineus"* and *P. "latifolius verrucosus."* In the United States specimens represented by these trade names were introduced by the Arnold Arboretum around 1910, and they were numbered in the field 4454-2 and 539-6. Meanwhile in the Cambridge Botanical Garden a plant of the same

species was cultivated under the name *P. hirsutus*. Cuttings from this plant were planted in the Arnold Arboretum under the field number 15358. It is very likely that both the European stock and the Cambridge planting of this species were introduced into cultivation by Gattinger, who practiced medicine in eastern Tennessee in the late 1800's and botanized that area very extensively. Some of his collections of a vegetatively similar species were labeled and distributed in outstanding American herbaria as *P. hirsutus*. Again in 1905 T. G. Harbison went to the type locality to collect specimens and seeds for the Arnold Arboretum. Specimen number 4454 was raised from Harbison's seeds.

18a. *Philadelphus inctectus* var. *pubigerus*, var. nov.

Frutex altus, ramulis cinereis vel plumbeis, hornotinis glabris; foliis ovatis vel ellipticis, supra glabris vel glabrescentibus, subtus uniforme strigoso-villosis, subintegris vel utrinque 1 vel 2 dentibus minutis; inflorescentiis 7- vel 9-floribus, paribus inferioribus in axillis foliorum positis; hypanthiis sepalisque glaberrimis, capsulis oboviedo-ellipsoideis; seminibus longicaudatis.

UNITED STATES: Arkansas: Baxter Co., Norfolk, *D. Demaree* 3071 (MO, US); Garland Co., Hot Springs, *E. J. Palmer* 26870 (A, MO); Le Flore Co., Page, *E. J. Palmer* 22623A (A, TYPE); Logan Co., Magazine Mountain, *D. Demaree* 17727 (MO), 21320 (NY); Marion Co., Rush, *E. J. Palmer* 6033 (A, MO); Pope Co., London, *H. E. Wheeler*, May 10, 1922 (F); Van Buren Co., Shirley, *E. J. Palmer* 25202 (A, MO).

This variety is distinguished from the typical *P. inctectus* Beadle by its pubescent leaves. In this respect it resembles *P. pubescens* Lois., but the latter species has pubescent hypanthia. Besides this morphological differentiation existing between this pubescent variety and the typical glabrous *P. inctectus*, there is also a geographical separation between them. *Philadelphus inctectus* was discovered on the steep rocky slopes and bluffs of the Cumberland River, and its present range is in the interior low plateau region, principally in the Nashville Basin and the Lexington Plain. *Philadelphus inctectus* var. *pubigerus* is restricted to the interior highland region. It occurs on the rim of bluffs on the top of Magazine Mountain or on the rocky bluffs of the Ouachita River. Geographically it is more closely associated with *P. pubescens* than with *P. inctectus*. Morphologically it serves as a link between these two species and a bridge between the *Gordoniani* series of the northwestern states and the *Pubescentes* series of the southeastern states of the United States.

19. *Philadelphus trichothecus*, sp. nov.

Frutex erectus, ramulis brunneis, bienniis 2-3.5 mm. diametro, cortice clauso, hornotinis strigoso-pilosis; foliis ovatis vel oblongo-ellipticis, 3-7 cm., raro usque 8.5 cm. longis, 1-3 cm. latis, basi rotundatis vel obtusis, apice breve acuminatis, acutis vel raro obtusis, supra ad nervos pilosis, aliter glabris, subtus barbatis et ad nervos strigoso-pilosis, subintegris vel

utrinque 2- usque 6-dentatis; inflorescentiis 5-, 7-, raro 3-floribus, bracteis foliaceis; hypanthiis sparse pilosis, sepalis ovato-oblongis, 8 mm. longis, basi 3.5 mm. latis, apice caudatis; corolla cruciformi, 3-4.5 cm. diametro, petalis oblongis, 17-20 mm. longis, 8-10 mm. latis, glabris; staminibus ca. 30, antheris hirsutis; disco et stylo glabris; capsulis obovoideis, 7 mm. longis, 6 mm. diametro; seminibus ignotis.

CANADA: British Columbia: Vancouver Island, Victoria, Oak Bay, *W. R. Carter* (G, TYPE); Fraser River at Hope, *C. L. Hitchcock & J. S. Martin* 7361 (MO, NY).

UNITED STATES: Washington: Ferry Co., Columbia River below Kettle Falls, *H. T. Roger* 558 (G, MO, NY); Klickitat Co., Bingen, *W. N. Suksdorf* 3704 (A); Mt. Constitution, *H. C. Cowles* 382 (G); Whatcom Co., *W. C. & W. W. Muenscher* 5430 (BH). Oregon: Clear Water, *Rev. Spalding*, May 28 (G); Portland, *F. A. Walpole* 2 (US); Oneonta Tunnel, *J. W. Thompson* 4710 (MO, US), Wasco Co., near Rice Station, *W. E. Lawrence* 122 (BH). California: Humboldt Co., Willow Creek, *L. R. Abrams* 7200 (NY); Siskiyou Co., *G. D. Butler* 1558 (MO, US); Trinity Co., Weaverville, *J. P. Harrington*, June 2, 1928 (US). Idaho: Boise River, *A. I. Mulford*, July 1892 (NY); Nez Perces Co., *J. H. Sandberg*, June 1892 (G); Capse, *G. B. Aiton* (MO). Montana: Garnet Co., *Mrs. E. W. Scheuber* 193 (F, NY, US).

CULTIVATED: Arnold Arboretum 22652, *R. B. Clark*, June 19, 1941 (BH).

Both in leaf form and in the sparsely pilose hypanthia this species resembles *P. lewisii* var. *helleri* (Rydb.) S. Y. Hu, but it can readily be distinguished from the latter taxon by its hirsute anthers.

20. *Philadelphus oreganus* Nuttall ex Torr. & Gray, Fl. N. Am. 1: 595. 1840, in syn., *nomen nudum*.

Philadelphus gordonianus sensu Torr. & Gray, l.c., pro parte, quoad spec. Nuttall, non Lindley.

TYPE: Oregon woods, Nuttall (G).

Frutex erectus, ramulis brunneis, biennii 3-4 mm. diametro, cortice clauso, hornotinis sparse pilosis, glabrescentibus; foliis late ellipticis, ovato-ellipticis vel ovatis, 5-8 cm. longis, 2-4.5 cm. latis, basi obtusis vel rotundatis, apice obtusis vel acutis, subintegris, supra sparse strigoso-pilosis, subitus praeter nervos glabris; inflorescentiis 7-, 9- vel 11-floribus, paribus inferioribus in axillis foliorum compositis, pedicellis 3-5 mm. longis, glabris; hypanthiis sparse pilosis; sepalis ovatis, 7 mm. longis, apice acuminatis; corolla cruciformi, 3.5 cm. diametro, petalis oblongis, apice rotundatis, 1.5 cm. longis, 1 cm. latis; staminibus ca. 35; margine disci solis vel disco et stylo pilosis; capsulis ellipsoideis, 7 mm. longis, 5 mm. diametro; seminibus longicaudatis.

UNITED STATES: Oregon: Portland, *A. Eastwood* 1132 (A); Oregon woods, Nuttall (G, TYPE; NY, ISOTYPE). California: Humboldt Co., Arcata, *A. A. Heller* 13776 (MO, NY, US); Dyerville, *H. H. Smith* 3928 (F, G,

NY, US); Trinity Co., Rush Creek, *H. S. Yates* in June 1914 (US). Idaho: Lake Pend d'Oreille, *E. L. Greene*, Aug. 8, 1889 (US).

21. *Philadelphus confusus* Piper, Bull. Torr. Bot. Club 29: 225. 1902.
—Koehne in Mitt. Deutsch. Dendr. Ges. 1904 (13): 81. 1904.—
Schneider, Ill. Handb. Laubh. 1: 367. 1905.—Rydb. in N. Am. Fl.
22: 166. 1905.—Rehder, Man. Cult. Trees Shrubs 272. 1927, ed.
2, 267. 1940; et Bibl. Cult. Trees Shrubs 191. 1949.

TYPE: Washington, Tum-Tum Mountain, *O. D. Allen* 221 (G).

An erect shrub, the second year's growth brown, 2-4 mm. in diameter, the bark closed, with few transverse cracks, the current year's growth glabrous, ciliate at the nodes. Leaves ovate-elliptic, 4-7 cm. long, 2-3 cm. wide, obtuse at both ends, subentire, glabrous on both surfaces except the principal nerves. Inflorescences 5-, 7-, rarely 3-flowered, the lower pairs in the axils of normal leaves; hypanthia subglobose, glabrous, the sepals ovate, 5-6 mm. long, acute at the apex; corolla cruciform, 2.5 cm. across, the petals oblong, 15 mm. long, 6 mm. wide, glabrous, the apex rounded; stamens ca. 25, anthers hirtellous at the base; disc sparsely pilose, style very short, with the stigmas 4 mm. long, spatulate. Capsules broad-ellipsoid, 6-8 mm. long, 5-6 mm. in diameter, the persistent calyx supermedian. Seeds long-caudate, the embryo cylindrical, 0.75 mm. long, the tail slightly longer.

UNITED STATES: Washington: King Co., Issaquah, *J. W. Thompson* 10522 (A, MO); Cascade Mountains, *Dr. Lyall* 1859 (G); Tum-Tum Mountain, *O. D. Allen* 221 (G, TYPE; A, MO, NY, US, ISOTYPES). California: Humboldt Co., Yager Road, *S. K. Harris* 3529 (G); *H. H. Smith* 3928 (G, MO). Idaho: Latah Co., Moscow, *M. Murley* 1734 (MO).

It is fitting to call this species *P. confusus*. There is no strong character to warrant it a distinct species, yet it is hard to amalgamate it with the other known species. It was described on the basis of three collections, namely, *Allen* 221 from Washington, *Sandberg, Heller and McDougal* 253 from Idaho, and *Brown*, July 16, 1896, from Oregon. *Brown's* collection, with its glabrous hypanthium, disk and anthers, is typical *P. lewisii* Pursh. *Sandberg, Heller and McDougal* 253 represents a mixture of fruiting and flowering material collected from different places as well as on various occasions. Some specimens of this number are *P. lewisii* and others are *P. lewisii* var. *helleri*. *Allen* 221 was designated as the type of the species. A year after the publication of the species, on the sheet deposited in the Gray Herbarium, Piper wrote, "This I made the type of *confusus* relying principally on the style character. I now regard this as unreliable and think the leaf pubescence furnishes on the whole the best distinction between *gordonianus* and *lewisii*. Dentation, style and bark characters seem to me more inconstant." Thus Piper invalidated his species. Rydberg and Rehder accepted this species, distinguishing it from *P. lewisii* by its yellowish or gray closed bark and acute sepals. Again these are variable characters. By employing a good binocular, hairs are observed on the style,

disk, and anthers of the type material. This suggests its relationship with *P. oreganus* Nutt., which has a pubescent disc, and *P. trichothecus* S. Y. Hu, which has hirtellous anthers.

22. *Philadelphus zelleri*, sp. nov.

Frutex erectus, ramulis brunneis, bienniis 3 mm. diametro, cortice clauso, hornotinis sparse villosis; foliis ovato-ellipticis, 3–6 cm. longis, 1.5–3 cm. latis, basi obtusis, rotundatis vel acutis, apice acutis vel breviter acuminatis, utrinque praeter nervos glabris; inflorescentiis 7- vel 9-floribus; hypanthiis calycibusque sparse pilosis; sepalis ovatis, 5–6 mm. longis, apice acutis; corolla cruciformi, 3–5 cm. diametro, petalis obovatis, utrinque hirtellis, 16–18 mm. longis, 9–10 mm. latis, apice erosis; staminibus ca. 35, antheris hirtellis; disco et stylo sparse pilosis; capsulis ignotis.

UNITED STATES: Washington: San Juan Island, Friday Harbor, *S. M. & E. B. Zeller* 974 (US, TYPE; fragment, A).

This is a very strange specimen. Of all the northwestern American material I have examined, this is the only one which has hirtellous petals. Its hirtellous anthers suggest a close relationship with *P. trichothecus* S. Y. Hu, but it can easily be distinguished from the latter species by its pubescent petals.

Series 2. *Tomentosi*, ser. nov.

Philadelphus subg. II. *Euphiladelphus* sect. 4. *Stenostigma* ser. 2. *Tomentosi*, ser. nov.

Philadelphus sect. *Stenostigma* subsect. *Satsumani* Koehne in Gartenfl. 45: 451, 561. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 82. 1904, pro parte.

Philadelphus sect. *Coronarii* (Koehne) Nakai in Bot. Mag. Tokyo 29: 64. 1915, pro parte.

Philadelphus ser. *Coronarii* (Koehne) Rehder, Man. Cult. Trees Shrubs ed. 2, 269. 1940; et Bibl. Cult. Trees Shrubs 192. 1949, pro parte.

TYPE SPECIES: *P. tomentosus* Wall. ex G. Don.

Frutices erecti, foliis ovatis, apice caudatis vel acuminatis, acumine 1.5–2.5 cm. longo, floribus racemosis, paribus inferioribus in axillis foliorum positis; corolla parva, 2–3 cm. diametro; staminibus 25 usque 38; stylo $\frac{1}{3}$ – $\frac{1}{2}$ diviso, faciebus stigmatum ventralibus saepe fissis; capsulis ellipsoideis vel obovoideis; caudis seminum brevibus vel elongatis.

This series is isolated in a small area of the western Himalayan region between Long. 77–79° E. and Lat. 30–33° N. There is no geographical isolation among the three included species. They all occur along the roads on the forested slopes at altitudes of 2000 to 3000 meters.

KEY TO THE SPECIES

A. Style glabrous.

B. Leaves tomentose beneath; seeds with long tails; hypanthia often with

few weak caducous villose hairs. 23. *P. tomentosus*.
 BB. Leaves glabrous beneath; seeds with short tails; hypanthia glabrous. 24. *P. triflorus*.
 AA. Style pubescent. 25. *P. lancifolius*.

23. ***Philadelphus tomentosus* Wall.**, Num. List, No. 3653. 1831, *nom. nud.* — G. Don, Syst. 2: 807. 1832, *descr.* — Royle, Ill. Bot. Himal. 1: 215. 1835; 2: *pl. 46, fig. 1*, 1839. — Loudon, Arb. Frut. Brit. 2: 955. 1838. — Walp., Repert. 2: 151. 1843. — Dippel, Handb. Laubh. 3: 338, *fig. 177*. 1893. — Koehne, Deutsche Dendr. 182. 1893; in Gartenfl. 45: 562. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 84. 1904. — Schneider, Ill. Handb. Laubh. 1: 371, *fig. 237c-e*. 1905. — Osmaston, For. Fl. Kumaon 230. 1927. — Rehder, Man. Cult. Trees Shrubs 275. 1927, ed. 2, 270. 1940; et Bibl. Cult. Trees Shrubs 192. 1949. — Engler, Pflanzenf. ed. 2, 18a: 194. 1930. — Bean, Trees Shrubs ed. 7, 2: 420. 1950; et in Chitt., Dict. Gard. 3: 1547. 1951.

Philadelphus nepalensis Wall. ex Loud., Hort. Brit. 196. 1830, *nom. nud.* — (*P. nipaulensis*) G. Don, Gen. Syst. 2: 807. 1832, in syn.

Philadelphus coronarius var. *tomentosus* Hook. f. et Thom. in Jour. Linn. Soc. Bot. 2: 83. 1857. — Maxim. in Mém. Acad. Sci. St. Pétersb. VII. 10 (16): 41 (Rev. Hydr. As. Orient. 41). 1867. — Clarke in Hook. f., Fl. Brit. Ind. 2: 407. 1878.

TYPE: *Wallich 3653A* (*Thomson* from *Gassain, Kew*).

Shrub 2–3 m. high, bark of second year's growth cinnamon, tardily exfoliating; current year's growth glabrous or glabrescent, 1.5–2 mm. in diameter. Leaves ovate, rarely lanceolate, 4–10 cm. long, 2–5 cm. wide, rounded or obtuse at the base, caudate at the apex, the acumen 1.5–2.5 cm. long, 5- or 7-nerved, glabrescent above, uniformly villose beneath, the trichomes compressed. Inflorescences pseudoracemose, 5- or 7-, rarely 3-flowered, the lower pairs usually in the axils of normal leaves, bracts to the terminal flowers often leafy, linear or lanceolate, up to 4 cm. long, 1 cm. wide, rather persistent; pedicels 6–11 mm. long, villose, hypanthium and calyx more or less glabrous, often with weak caducous villose hairs; sepals ovate, 5 mm. long, 3 mm. wide, acuminate; corolla cruciform, 1.5–2.5 cm. across, the petals obovate-oblong, 0.5–1 cm. long, 5–8 mm. wide; stamens about 25, the longest 8 mm. long; disk glabrous, the style 7 mm. long, the upper one third divided, the stigma clavate, the abaxial surface definite, 1–1.5 mm. long, the adaxial surface 3 or 4 times longer, often split at the middle. Capsule ellipsoid, 1 cm. long, 6–7 mm. in diameter, the persistent sepals supermedian. Seeds with medium-long tails.

INDIA: Chamba State: Camba Range, *R. N. Parker*, June 6, 1919 (A); Pangi, June 1919 (A); Alwas, *R. R. Steward* 2512 (A, NY). Garhwal: Panikhanada, Phagti, *A. E. Osmaston* 382 (A); same area, *H. Falconer* 470 (G, NY). Siwalik & Jaunsar Divisions: Chakrata Amar Chand 44 (NY). Kumaon: *R. Strachey & J. E. Winterbottom*, C (G). Kulu Himalaya: Puling, *W. Koelz* 284 (NY). Himal. Bor. Occ. Regio

Temp. : *T. Thomson*, alt. 7–10,000 ft. (G, NY); *T. Thomson*, alt. 6–9000 ft., A (G).

CULTIVATED: Europe: Kew, G. Nicholson 1317. United States: Arnold Arboretum nos. 15419 (= 2482–2 — from Germany), 4785 (from Kew), 15422 (4785–3) (all in A).

One of the Thomson collections and the Strachey and Winterbottom collection both represent mixtures of different elements in the Gray Herbarium. On the Thomson sheet there are two specimens. "A" represents a shoot with three fruits. Its leaves are tomentose and it belongs to this species. "B" is a flowering specimen of *P. triflorus* Wall. Its leaves are glabrous beneath, except the principal nerves, which are sparsely villose. The Strachey & Winterbottom sheet has three elements. A is a fruiting specimen. B and C are flowering specimens. The lower surface of the leaves of A and B is glabrous, except the principal nerves, beneath. They are *P. triflorus* Wall.

Philadelphus tomentosus Wall. was established on the basis of three collections from Gassain, Simore, and Kumaon of the western Himalayan region. It was validated by G. Don's description published in 1832. According to this description, the species has ovate acuminate leaves which are tomentose beneath. I have not seen the syntype. Among the more recent collections, the specimens that fit Don's description in the leaf character all have more or less glabrous hypanthia, low stamen count, glabrous disk and style, clavate stigma with the abaxial surface often split, ellipsoid fruit, and long-tailed seeds.

Philadelphus tomentosus Wall. is restricted to the western Himalayan region. Koehne in 1904 recorded it from Japan. There is some mistake in his identification. In the western Himalayan region the plants occur generally in shady forests at altitudes of 2100–2800 meters. The white, fragrant flowers appear in May in some areas and in June or July in other places.

According to Loudon, *P. tomentosus* Wall. was introduced into cultivation in 1822. It is a species with comparatively small flowers. Among the cultivated examples I have seen material prepared from the Arnold Arboretum, Kew, Hort. Plantières, Hort. Les Barres, Hort. Späth, etc. According to my understanding of the species, only the material from the first two institutions is true to the type of the species.

24. *Philadelphus triflorus* Wall., Num. List 3653. 1831, *nomen nudum*. — Royle, Ill. Bot. Him. 1: 215. 1835, *nomen subnudum*. — Loudon, Arb. Frut. Brit. 2: 955. 1838, in syn. — Koch in Wochenschr. Gärtn. Pfl. 2: 228. 1859, in syn.

Philadelphus nepalensis Koehne, Dendr. 183. 1893; in Gartenfl. 45: 618. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 85. 1904. — Schneider, Ill. Handb. Laubh. 1: 373, fig. 238g. 1905. — Rehder, Man. Cult. Trees Shrubs 276. 1927; ed. 2, 270. 1940; et Bibl. Cult. Trees Shrubs 192. 1949, non Wall. ex Loudon 1830.

TYPE: *Wallich 3653B* (Kew).

Erect shrub, bark of the second year's growth light brown, tardily exfoliating, the current year's growth glabrous. Leaves ovate, 6–9 cm. long, 3–5 cm. wide, rounded or obtuse at the base, caudate at the apex, the acumen 15–25 mm. long, glabrous above, entirely glabrous or the principal nerves sparsely pubescent beneath. Inflorescences racemose, 5- or rarely 3- or 7-flowered, the lower pairs in the axils of the normal leaves, the bracts of the terminal flowers linear or narrow-lanceolate, up to 3 cm. long, 4 mm. wide; pedicels (5-) 10–15 mm. long, glabrous or glabrescent; hypanthium and calyx glabrous; sepals ovate, 5 mm. long, 3 mm. wide, acuminate at the apex; corolla subdisciform, 2–3 cm. across, the petals ovate, 1–1.4 cm. long, 0.8–1.2 cm. wide; stamens 35–38, the longest 8 mm. long; disc and style glabrous, the latter 6 mm. long, the upper one third or half divided; stigma clavate, the abaxial surfaces 1.5 mm. long, the adaxial ones slightly longer, split. Capsules obovoid, 8 mm. long, 6 mm. in diameter, the persistent sepals subapical. Seeds with very short tails, the testa fuscous, reticulate, and more or less rugose.

NORTHERN INDIA: Chamba State: between Kukti and Hursa, *W. Koelz 867* (NY). Punjab: Bashahr State, Simla district, in forest at Bhali, *R. N. Parker 3034* (A); near Sangla, *M. V. Laurie 3579* (A); Kulu, *W. Koelz 1981* (NY). Garhwal: Tihri, Jumna Valley, data on label obscure (A). Kumaon: *Wallich 3653C* (*R. Brown*, Kew); *R. Strachey & J. E. Winterbottom* (A, BH, G). Himal. Bor. Occ. Regio Temp.: *T. Thomson* (BH, G). Simore: *Wallich 3653B* (TYPE, Kew).

CULTIVATED: Europe: Hort. Bot. Berol., *E. Koehne 467* (A, G, ISOTYPE of *P. nepalensis* Koehne); Hort. Münkau, *A. Rehder 405* (A); Hort. Späth, *C. K. Schneider* in 1902 (A). United States: Arnold Arboretum 6004, *C. E. Faxon*, June 21, 1910 (A), June 14, 1911 (A); *A. Rehder*, July 18, 1918 (A), June 30, 1920 (A); Arnold Arboretum 15419 = 810–42, *S. Y. Hu*, June 13, 1951 (A).

When Wallich first recorded the Himalayan *Philadelphus*, he cited three collections under two binomials, *P. tomentosus* and *P. triflorus*. His list number 3653A was from Gossainthan, 3653b from Simore, and 3653C from Kumaon. G. Don validated *P. tomentosus* Wall. in 1832 by giving it a description in which he characterized that species as having ovate leaves which are acuminate, denticulate, and tomentose beneath. In 1835 Royle doubtfully suggested *P. triflorus* Wall. as a juvenile form of *P. tomentosus* Wall. From that time *P. triflorus* Wall. has been treated as a synonym of *P. tomentosus* Wall. In 1893 Koehne described *P. nepalensis* on the basis of a plant cultivated in the Botanical Garden in Berlin, and characterized it as a species with leaves glabrous except the principal nerves beneath. A few years later, in a discussion about that species, he suggested that *P. triflorus* Wall. might belong to the same taxon. If this is true, the glabrous Himalayan species should be called *P. triflorus* Wall. and not *P. nepalensis* Koehne, for the latter binomial is preoccupied. Through the kindness of Dr. N. L. Bor, Assistant Director of the Royal Botanic Gardens,

Kew, this supposition has been confirmed. Dr. Bor kindly asked Mr. L. L. Forman to examine the specimens of *Philadelphus* in the Wallich herbarium for me. According to his report *Wallich 3653A*, a fruiting specimen, labeled *P. tomentosus* Wall., has leaves pubescent below. This specimen should be the type of the species as validated by G. Don. *Wallich 3653B*, labeled *P. triflorus* Wall., has leaves, hypanthium, style and disk all glabrous. Thus there is no doubt as to what Wallich meant for *P. triflorus*. It is different from *P. tomentosus* Wall. and conspecific with *P. nepalensis* Koehne. Mr. Forman also remarked that *Wallich 3653C*, another fruiting specimen, labeled *P. tomentosus* Wall., has glabrous leaves and it appears to equal *3653B*.

This species is undoubtedly closely related to *P. tomentosus* Wall. Geographically and ecologically they cannot be separated. But morphologically *P. triflorus* Wall. has leaves glabrous beneath. At first I suspected the glabrous Himalayan element to be a variety of *P. tomentosus* Wall. But when I saw the very short-tailed seed of a specimen with glabrous leaves, I inclined toward keeping it as a distinct species. In a seed of *P. tomentosus* Wall. the testa is ochraceous and the tail is as long as the embryo. In *P. triflorus* Wall. the testa is fuscous and the tail is one fourth the length of the embryo.

This species has long been cultivated in Europe. *Rehder 405* was collected as early as 1888. In American gardens some specimens of this species are cultivated under the name *P. tomentosus*. The plants distributed by the Park Department of Rochester under the name *P. "magnificus"* definitely belong here.

The cultivated specimens all have castaneous exfoliating branchlets and the axils of the principal nerves barbate. In this respect they differ slightly from the spontaneous material, which has light brown bark and glabrous nerve angles beneath.

25. *Philadelphus lancifolius* Koehne in *Gartenfl.* 45: 561. 1896; et in *Mitt. Deutsch. Dendr. Ges.* 1904 (13): 82. 1904. — *Engler, Pflanzenfam.* ed. 2, 18a: 194. 1930.

TYPE: *C. B. Clarke 46543* (British Museum).

Shrub with grayish brown bark on the second year's growth. Leaves ovate or ovate-lanceolate, 4–7 cm. long, 1–3 cm. wide, caudate, the acumen about 2 cm. long, dentate, with 3–7 teeth on each side, 7-nerved, the lower surface thickly tomentose. Inflorescences pseudoracemose, 7- or 9-flowered, loose, the lower pairs in the axils of normal leaves. Flowers not known. Fruiting pedicels 1–1.5 cm. long; capsules obovoid, about 8 mm. long, 6 mm. in diameter, the persistent sepals super-median, the remaining basal portion of the style pubescent (according to Koehne). Seed not seen.

NORTHERN INDIA: *Kumaon*: *R. Blinkworth*, ex *Herb. C. B. Clarke 46543* (photograph of **TYPE**, A).

The foregoing description is a synthesis of characters that can be detected from a photograph of the type and those given by Koehne. In describing

the shape of the leaves Koehne used the words "länglich oder länglich-lanzettlich." I do not choose to employ the English equivalents of these words, for the leaves in the photograph of the type appear ovate or ovate-lanceolate to me.

The type is a fruiting specimen with the capsules all open and the styles broken off. Koehne observed hairs on the remaining basal portion of the style. By this character of the hairy style *P. lancifolius* Koehne is distinguished from its closely related species *P. tomentosus* Wall. *Philadelphus lancifolius* Koehne is known only from the type collection. Among all the Himalayan material that I have examined, I have seen no specimen with pubescent style. Although molds have been mistaken for hairs by eminent botanists, I hesitate to doubt Koehne's observation, for individuals with a pubescent style have been found in the natural populations of many regions, and they may also occur in western Himalaya. According to my understanding of the permanence of the stylar hairs in species like *P. schrenkii* Rupr., I know that although the hairs are delicate, they are persistent and can be observed even on mature fruit. If the species does have a pubescent style, even though Koehne's material is rather advanced in age, his observation was not impossible.

Series 3. *Pekinenses*, ser. nov.

Philadelphus subg. II. *Euphiladelphus* sect. 4. *Stenostigma* ser 3. *Pekinenses*, ser. nov.

Philadelphus sect. *Stenostigma* subsect. *Coronarii* Koehne in Gartenfl. 45: 451, 596. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 84. 1904, pro parte.

Philadelphus sect. *Coronarii* (Koehne) Nakai in Bot. Mag. Tokyo 29: 64. 1915, pro parte.

Philadelphus ser. *Coronarii* (Koehne) Rehder, Man. Cult. Trees Shrubs ed. 2, 269. 1940; et Bibl. Cult. Trees Shrubs 192. 1949.

TYPE SPECIES: *P. pekinensis* Rupr.

Frutices saepe humiles, foliis ovatis vel ovato-ellipticis, apice acuminate; inflorescentiis 5- usque 7-floris, hypanthiis glabris; corolla praesertim parva, 2-3 cm. (raro 3.5 cm.) diametro; staminibus 25 vel 30, raro plus; disco et stylo glabris, stigmatibus spatulatis vel clavatis, faciebus dorsaliibus brevissimis; capsulis subglobosis vel ellipsoideis; seminibus breviter vel mediano-caudatis.

Species of this series are concentrated in the North China uplands, including Johel, Hopei, Shansi, Shensi, and southern Kansu, and north-western Hupei. One species occurs in the hills outside Nanking, and its variety is found in the uplands of western Chekiang, Kiangsi and southern Anhwei.

KEY TO THE SPECIES OF THE SERIES

A. Seeds very shortly caudate, the tails shorter than the embryo; capsules subglobose, the persistent sepals apical; rachis 0.2-1.5 cm. long; leaves glabrous on both surfaces. 26. *P. pekinensis*.

AA. Seeds medium caudate, the tail as long as the embryo; capsules ellipsoid, the persistent sepals supermedian; rachis 2-12 cm. long; leaves strigose on the principal nerves beneath.

B. Leaves very sparsely strigose above; style spatulate, the tail of the seed as long as the embryo; bark of the second year's growth brownish gray, closed. 27. *P. brachybotrys*.

BB. Leaves uniformly setose above, the trichomes compressed; style clavate; the tail of the seed half as long as the embryo; the second year's bark castaneous, exfoliate. 28. *P. laxiflorus*.

26. *Philadelphus pekinensis* Ruprecht in Bull. Phys.-Math. Acad. Sci. St. Pétersb. 15: 365. 1857; et in Mél. Biol. 2: 543. 1858. — Koehne in Gartenfl. 45: 597. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 84. 1904. — Bretschneider, Hist. Eur. Bot. Discov. China 349, 1054. 1898. — Schneider, Ill. Handb. Laubh. 1: 373, fig. 273, *p-r* et 238, *e-f*. 1905. — Silva Tarouca, Freidland-Laubgeh. 283, fig. 351. 1913; et 255, fig. 309. 1930. — Nakai in Bot. Mag. Tokyo 29: 65. 1915; et Fl. Sylv. Kor. 15: 50. 1926. — Limprecht in Fedde, Repert. Sp. Nov. Beih. 12: 402 (Bot. Ergeb. Reis. Hochgeb. Chin. Ost.-Tib.). 1922. — H. H. Hu, Ic. Pl. Sin 1: 29 1927. — Rehder in Jour. Arnold Arb. 5: 151. 1924, 8: 113. 1927, 12: 275. 1931; Man. Cult. Trees Shrubs 276. 1927; ed. 2. 270. 1940; et Bibl. Cult. Trees Shrubs 193. 1949. — Liu in Bull. Pek. Soc. Nat. Hist. II, 3: 104. 1925. — Minami, List Pl. Manch. Mong. 183. 1926. — Chen, Ill. Man. Chin. Trees Shrubs 373, fig. 279. 1937. — Kitagawa, Lin. Fl. Mansh. 253. 1939. — Sata, Ill. Manch. Mong. Trees ed. 2, 128. 1943. — Bean, Trees Shrubs ed. 7, 2: 417. 1950; et in Chitt, Dict. Gard. 3: 1546. 1951.

Philadelphus coronarius sensu Turcz. in Bull. Soc. Nat. Moscou X, 7: 151. 1837. — Maxim. in Mém. Div. Sav. Acad. Sci. St. Pétersb. 9: 471 (Ind. Fl. Pekin.). 1859, non Linn. 1753.

Philadelphus coronarius Linn. var. *pekinensis* Maxim. in Mém. Acad. Sci. St. Pétersb. Ser. VII, 10 (16): 42 (Rev. Hydrang. As. Or. 42). 1867. — Franch. in Nouv. Arch. Mus. Hist. Nat. Paris II, 6: 5 (Pl. David. 125). 1883. — Forbes & Hemsl. in Jour. Linn. Soc. Bot. 23: 278. 1887.

Philadelphus parviflorus Carr. in Rev. Hort. 1870: 460. 1870.

Philadelphus rubricaulis Carr. in Rev. Hort. 1870: 460. 1871. — Bretschneider, Hist. Eur. Bot. Discov. China 830. 1898. — Rehder, Man. Cult. Trees Shrubs 276. 1927; ed. 2, 270. 1940; et Bibl. Cult. Trees Shrubs 193. 1949, ? in syn.

Deutzia chaetetii Lévl. in Fedde, Repert. Sp. Nov. 9: 451. 1911. — Rehder in Jour. Arnold Arb. 12: 275. 1931, in syn.

TYPE: *P. Y. Kirilov*, hills west of Pekin (Herb. Acad. Sci. St. Pétersb.).

A graceful, low, compact shrub up to 2 m. high, bark of second year's growth castaneous, exfoliating; current year's growth glabrous. Leaves ovate, those on the sterile shoot 6-9 cm. long, 2.5-4.5 cm. wide, obtuse or rounded at the base, long-acuminate at the apex, the acumen 2-2.5 cm. long, serrate, glabrous on both surfaces, occasionally bearded in the nerve

axils beneath, 5-nerved; those on the flowering shoot 3-4, rarely up to 7 cm. long, 1.5-2.5 cm. wide, glabrous on both surfaces, bearded in the axils of the principal nerves beneath, serrate, rarely subentire. Inflorescences 5-, 7-, 9-, rarely 3-flowered, the lowest pair of flowers often in the axils of normal leaves, the rachis 2-15 mm. long, the bracts linear, 3-4 mm. long, 0.5 mm. wide, ciliate, the pedicels 3-6 mm. long, glabrous; hypanthium and calyx glabrous; sepals ovate, 4 mm. long, 2.5 mm. wide, acuminate; corolla discoid, 2-3 cm. across, the petals obovate, 9-11 mm. long, 8 mm. wide; stamens 25, the longest 5-7 mm. long; disk and style glabrous, the style 4-5 mm. long, the upper one fifth to one fourth divided, the stigma subspatulate, the apical end enlarged, the abaxial surface short and broad, 1 mm. long, the adaxial ones three times as long. Capsules subglobose or obconic, 5-7 mm. in diameter, the persistent sepals subapical. Seeds short-tailed.

CHINA: Johel: *A. David* 2219 (G); Wei-chang, *Wm. Purdom* 83 (A). Hopei (Chihli): Peking and vicinity, Western Hills, *J. Hers.* 2515 (A), 2225 (A); Po-hau-shan, *J. Hers.* 1462 (A), 1680 (A); same locality, *W. Y. Hsia* 2144 (NY); Miao-feng shan, *J. Hers.* 2539 (A); Peking & Kalgan Road, hills near Great Wall, *J. G. Jack*, Oct. 5, 1905 (A); Kalgan Valley, *F. T. Wang* 20262 (NY); Men tou-kou, *T. F. King* 2 (NY); Ling-shan, *T. F. King* 626 (A, NY); Paefeng-tzi, *C. W. Wang* 60802 (A); (Tche-Ly) mont du Kouying, *L. Chanet* 416 (HOLOTYPE of *Deutzia chanetii* Lévl., A); Hsiao-wu-tai shan, *J. Hers.* 1476 (A), 2183 (A), 2185 (A); same locality, *J. C. Liu* 1889 (NY); *F. M. Meyer* 1304 (A); *H. Smith* 313 (A); *C. W. Wang* 6165 (A); *T. P. Wang* 482 (NY); without precise locality, *L. Chanet* 61 (A). Shensi: Wu-tai shan, *J. Hers.* 2642 (A); Ja siu, *C. T. Ren* ex Univ. of Nanking Herb. no. 6123 (A); Mien shan, *R. W. Chaney* 1069 (NY). Szechuan: Teng-hsiang-ying, *H. Smith* 186 (A), 1935 (A).

CULTIVATED: Europe: Hort. Bot. Berol., *E. Koehne* 1904, 466 (A); Hort. Vilmorin; Plantière *C. Schneider* 1906. United States: Arnold Arboretum field no. 1769 (seed received from Bretschneider, flowered June 28, 1888); no. 1223 (introduced from Vilmorin, flowered in June 1899; no. 6596 (seed received from *W. Purdom*, Lot no. 174, flowered in June 1915), *S. Y. Hu*, June 1950. All this cultivated material has reddish brown nerves and petioles.

So far as I know the typical *P. pekinensis* Rupr. has been introduced to the western world on three occasions. Each introduction was in the form of seeds. The first came from E. M. Simon, who was collecting seeds in the hills west of Peking in 1862. These were sent to Paris in 1865. Plants raised from these seeds have reddish violet shoots, petioles, and nerves. Carrière in 1871 named the plant *P. rubicaulis*. The second introduction was by Bretschneider, who collected on the hills west of Peking in 1881-2. He sent the seeds to C. S. Sargent at the Arnold Arboretum, and also to Kew in England. Thus the living specimen now growing in the Arnold Arboretum is one of the oldest plants of this oriental species to be introduced into the western world. William Purdom collected seeds and specimens for the Arnold Arboretum in the mountainous area west and north of Peking, and his collections formed the third introduction of

this species. Plants raised from his seed, Lot no. 174, were first numbered Arnold Arboretum 6596, and later 20086. These plants first flowered in June 1915.

This species is a graceful compact shrub with the stems hidden by leafy branchlets. The current year's growth and the petioles are reddish brown. Just before the flowers open the buds have reddish purple stripes on the back. At anthesis the flowers are yellowish white with a pleasant fragrance. Many of the anthers bear no pollen. J. Hers recorded that in northern Shansi the people collect the young shoots and eat them as greens.

26a. *Philadelphus pekinensis* Rupr. f. *lanceolatus*, forma nov.

Frutex, ramulis glabris; foliis lanceolatis, 4–6.5 cm. longis, 1–2 cm. latis, basi cuneatis vel acutis, apice acuminatis, utrinque glabris, axilla nervorum barbatis; inflorescentiis 7-vel 9-floris, rhachibus 0.8–1.5 cm. longis, corolla subdisciformi, 2 cm. diametro.

CHINA: Hopei (Chihli): Hsiao-wu-tai-shan, C. F. Li 10522 (NY, TYPE).

This form differs from typical *P. pekinensis* Rupr. in having lanceolate leaves. According to the field label the type material was collected in August. It was in full bloom. Thus it is the latest blooming form known to the Old World.

27. *Philadelphus brachybotrys* Koehne ex Vilmorin & Bois, Frut. Vilm. Cat. Prim. 128. 1904. — Koehne in Sargent, Pl. Wils. 1: 5. 1911. — Bean, Trees Shrubs ed. 7, 2: 417. 1950.

Philadelphus pekinensis Rupr. var. *brachybotrys* Koehne in Mitt. Deutsch. Dendr. Ges. 1904 (13): 84. 1904. — Rehder, Man. Cult. Trees Shrubs 276. 1927; ed. 2, 270. 1940; et Bibl. Cult. Trees Shrubs 193, 1949.

TYPE: *M. L. de Vilmorin* (Herb. E. Koehne).

A large shrub up to 3 m. high, the bark of the second year's growth brownish gray, close; the current year's growth villose, becoming glabrescent. Leaves ovate, 2–6 cm. long, 1–3 cm. wide, rounded or obtuse at the base, shortly acuminate or acute at the apex, finely serrate or subentire, sparsely strigose above, strigose on the nerves beneath. Inflorescences 5- or 7-flowered, the lower pair of flowers often in the axils of normal leaves, the rachis 2–4 cm. long, sparsely villose, pedicels 3–5 mm. long, sparsely strigose, becoming glabrescent, hypanthium and calyx glabrous; sepals ovate, 4–6 mm. long, 3–4 mm. wide, acuminate; corolla cream-white, disciform, 2.5–3.5 cm. across, the petals suborbicular 1–1.5 cm. long, 1–1.3 cm. wide; stamens 31–40, the longest 8 mm. long; disc and style glabrous, the style subequal to the long stamens, the apical one third divided, the stigma spatulate, the abaxial surface 1 mm. long, the adaxial twice as long, narrowed gradually. Capsules ellipsoid, 7–10 mm. long, 5–7 mm. in diameter, the persistent calyx supermedian. Seeds short-tailed, the embryo 1–5 mm. long, the tail equaling the embryo in length.

CHINA: Kiangsu: Nanking, Ox-head mountains, in woods, *C. L. Tso* 991 (A).

CULTIVATED: Arnold Arboretum no. 6596 (plant from Hort. Vilmorin, 1901), *A. Rehder*, June 18, 1908 (A); Hort. C. S. Sargent (Vilmorin), *A. Rehder*, June 26, 1909 (A); (Pl. L. Späth, Berlin), *A. Rehder* 104 (A).

This species can be distinguished by its pubescent current year's growth, close brownish gray bark of the two-year-old branchlets, sparsely strigose leaves, short rather crowded inflorescence and suborbicular petals. It was first established on the basis of a plant cultivated in the garden of M. L. de Vilmorin in France. According to the records supplied to Koehne by Vilmorin, it was raised from seed sent to him by a Father Mouton from Tschen-Kéu, Kiangsi Province. I have not been able to learn anything about this French missionary, nor could I find any place in Kiangsi that sounded like Tschen-Kéu. Thus it is impossible for me to supply the exact place of origin of this species in China. *C. L. Tso* 991 from Kiangsu is the only spontaneous material which fits Koehne's description for this species and matches the specimen collected from plants sent us from Hort. Vilmorin. It is closely related to *P. pekinensis* Rupr., a glabrous species of the North China highlands.

27a. *Philadelphus brachybotrys* Koehne var. *laxiflorus* (Cheng), comb. nov.

Philadelphus pekinensis Rupr. var. *laxiflorus* Cheng in Contr. Biol. Lab. Sci. Soc. China 10: 113. 1936.

LECTOTYPE: *T. Tang & W. Y. Hsia* 383 (A).

Shrub up to 6 m. high, the second year's growth grayish brown or castaneous, closed, the current year's growth glabrous; leaves ovate, 4-9 cm. long, 2-4.5 cm. wide, obtuse, acute or on sterile shoots rounded at the base, acuminate at the apex, the acumen 5-10 mm. long, serrate, sparsely strigose or glabrescent above, strigose on the principal nerves beneath; racemes loose, 5-, 7-, 9-flowered, the rachis 4-8 cm. long, glabrous, pedicels 5-8 mm. long, after fruiting up to 11 mm. long.

CHINA: Chekiang: Tien-mo shan, *T. Tang & W. Y. Hsia* 383 (A, LECTOTYPE); same mountain, *H. H. Hu* 1551 (A), 1653 (A); West Lake, *H. H. Hu* 1497 (A); Yun-huo, *S. Chen* 1526 (A); Yen-tang shan, *C. Y. Chiao* ex Herb. Univ. Nanking no. 14682 (A); Chen-chiong, 40 miles south of Sia-chu, *R. C. Ching* 1740 (NY). Anhwei: Whang shan, *R. C. Ching* 2923 (A), 3005 (A).

CULTIVATED: Nanking, First Agriculture School, *Chen* 2549 (A).

This variety appears to be common in the woods of the mountainous areas in Chekiang. Cheng cited 23 collections from ten different localities of that province. It is also common in southern Anhwei. In these provinces the plants occur in open thickets by rocky cliffs or shady woods at altitudes of 300 up to 1500 meters. The white fragrant flowers appear in June and the early part of July.

28. *Philadelphus laxiflorus* Rehder in Jour. Arnold Arb. 5: 152. 1924.

Shrub 2–3 m. high, the bark of two years' growth grayish brown or castaneous, exfoliating; current year's growth glabrous, fuscous. Leaves ovate-elliptic or elliptic, 3–8 cm. long, 1.5–3 cm. wide, on weak branches sometimes 2 cm. long, 0.8 cm. wide, acute, obtuse, or on vegetative branches rounded at the base, acuminate at the apex, the acumen 5–15 mm. long, finely serrate, uniformly setose above, the hairs compressed, sparsely villose on the principal nerves beneath, often bearded. Inflorescences 7-, 9-, or 11-flowered, the lower pairs of flowers in the axils of normal leaves, the rachis 6–12 cm. long, glabrous; pedicels 6–10 mm. long, glabrous; hypanthium and calyx glabrous; sepals ovate, 6 mm. long, 4 mm. wide, acuminate; corolla disciform, 2.5–3 cm. across, the petals suborbicular, 1.6 cm. in diameter; stamens 30–35, the longest 9 mm. long; disc and style glabrous, the style as long as the longest stamens, the upper one third divided, the stigma clavate, the abaxial surfaces 1.8 mm. long, the adaxial twice as long, narrowed gradually. Capsules ellipsoid, 8 mm. long, 6 mm. in diameter, the persistent sepals supermedian. Seeds short-tailed, the tails half as long as the embryo.

CHINA: Shensi: Fang-shan Hsien, Nan-yang Shan, *J. Hers* 2704 (A). Shensi: Tsingling, 60 km. south of Sian, *J. Hers* 2959 (A); Tai-pei Shan, *Wm. Purdom* 439 (TYPE, A). Kansu: Kwan Shan, *G. Fenzel*, May 22–29, 1935 (A). Hupei (Hupé): Monte Si-ho (On-tang Scian), *P. C. Silvestri* 3004 (A); without precise locality, *P. C. Silvestri* 4358a (A, photo & fragment), 4359 (fragment, A); 4360 (fragment, A); Poa-ken, *P. C. Silvestri* 4361 (A); Scian-kin, *P. C. Silvestri* 4363 (A).

CULTIVATED: United States: New York: Highland Park, *E. H. Costich*, June 7, 1916 (A). Massachusetts: Hort. *C. S. Sargent*, June 3, 1913 (A).

This species is distinguished by its exfoliating castaneous bark, uniformly setose leaves, loose inflorescences, glabrous pedicels, clavate stigma, ellipsoid fruit, and short-tailed seeds. Its glabrous hypanthium suggests close relationship with *P. pekinensis* Rupr. But the latter species has glabrous leaves, crowded inflorescences, and globose fruits. Both morphologically and geographically this species is intermediate between *P. pekinensis* Rupr. and *P. sericanthus* Koehne. The pubescence of its leaves resembles that of *P. sericanthus* Koehne, but Koehne's species has pubescent hypanthia. It is probably a natural hybrid of a northern species with some southern influence. It occurs in woods at altitudes of 1500–2000 meters in the Tsingling mountains, and its range extends northward along the Shensi and Kansu border, reaching the Lu-liang mountains. Its white flowers appear in June.

Silvestri's collections from the eastern end of the Tsingling Range have been named and distributed under some unpublished binomials of Pampanini.

Series 4. *Coronarii* (Koehne) Rehder

Philadelphus subg. II. *Euphiladelphus* sect. 4. *Stenostigma* ser. 4. *Coronarii* (Koehne) Rehder, Man. Cult. Trees Shrubs ed. 2, 269. 1940; et Bibl. Cult. Trees Shrubs 192. 1949.

Philadelphus sect. *Stenostigma* subsect. *Coronarii* Koehne in Gartenfl. 45: 451, 596. 1896.

TYPE SPECIES: *P. coronarius* Linn.

Upright arching or dwarf compact shrubs, the bark of the second year's growth exfoliate; leaves ovate, elliptic or lanceolate, serrate or subentire; inflorescences 5- up to 9-flowered, rarely ternate; hypanthia glabrous, rarely with a few crisp weak hairs; corolla varied, disciform or cruciform, many doubled; stamens 21-25; style divided; capsules turbinate; seed with medium-long tails.

This series covers all the European and Caucasian elements. Due to the long period of cultivation and through controlled hybridization of growers or accidental crosses of remote species brought into close association in gardens, many hybrids and garden varieties are now in existence.

KEY TO THE SPECIES

- A. Leaves ovate or elliptic; petals glabrous at the apex.
 - B. Disc and style glabrous. 29. *P. coronarius*.
 - BB. Disc and style pubescent. 30. *P. caucasicus*.
 - AA. Leaves lanceolate; petals hirtellous at the apex; rim of the disc hirsute; style glabrous. 31. *P. salicifolius*.
- 29. ***Philadelphus coronarius* Linn.**, Sp. Pl. 470. 1753.—Kniphof, Bot. Orig. Herb. Viv. 5: pl. [65]. 1758.—Miller, Dict. Gard. ed. 8, [834]. 1768.—Hoppe, Ect. Pl. Ratisb. pl. 522. 1790.—Schmidt, Oest. Allgem. Baumzucht 1: 57, pl. 59, 60. 1792.—Curtis, Bot. Mag. 11: pl. 391. 1797.—Sturm, Deutschl. Fl. 1 (1): pl. [37]. 1798.—Lamarck, Ill. Planches Bot. pl. 420. 1791.—Willd., Sp. Pl. 2: 947. 1800.—D.C., Prodr. 3: 205. 1828.—Schrader in Linnaea 12: 388. 1838.—Loudon, Hort. Brit. 196. 1832; et Arb. Frut. Brit. 2: 951. 1838.—G. Don, Gen. Syst. 2: 807, fig. 114. 1832.—Schnizlein, Iconogr. 4: pl. 264. 1843.—Maxim. in Mém. Acad. Sci. St. Pétersb. VII. 10 (16): 36 (Rev. Hydrang. As. Or.). 1867.—Le Maout & Decaisne, Traité Gén. Bot. 260. 1868.—Koch, Dendrol. 336. 1869.—Boiss., Fl. Orient 2: 814. 1872.—Lavallée, Arb. Segrez. Enum. 114. 1877.—Hoffmann, Pflanzenatlas, pl. 39, fig. 244. 1881.—Nicholson, Ill. Dict. Gard. 3: 95, fig. 105. 1886.—Engler, Pflanzenf. III. 2a: 70. 1890; ed. 2, 18a: 191. 1930.—Koehne, Deutsche Dendr. 182. 1893; in Gartenfl. 45: 618. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 85. 1904.—Dippel, Handb. Laubh. 3: 335. 1893.—Nicholson in Kew Hand-List 1: 225. 1894; ed. 2, 373. 1902.—Fiori & Paol., Ic. Fl. Ital. 195, fig.

1696. 1895; et Fl. An. Ital. 1: 544. 1895.— Britt. & Brown, Ill. Fl. N. States Can. 2: 186. 1897; ed. 2, 232. 1913.— Rydb. in N. Am. Fl. 22: 164. 1905.— Merino, Fl. Descr. Ill. Gal. 1: 477. 1905.— Syereishtchikof, Ill. Fl. Mosc. 2: 220, fig. 1. 1907.— Pereira, Fl. Port. 284. 1913.— Bonnier, Fl. Compl. France Suisse Belg. 4: 40, pl. 194. 1921.— Hegi, Ill. Fl. Mittel.-Eur. IV. 2: 640, fig. 978. 1922.— Liu in Bull. Pek. Soc. Nat. Hist. 2 (3): 103. 1925.— Rehder, Man. Cult. Trees Shrubs 277. 1927; ed. 2, 271. 1940; et Bibl. Cult. Trees Shrubs 193. 1949.— Chen, Ill. Man. Chin. Trees Shrubs 374, fig. 280. 1927.— Bean, Trees Shrubs, ed. 7, 2: 411, pl. 34. 1950; et in Chitt. Dict. Gard. 3: 1546. 1951.

Frutex coronarius Clus., Hist. 1: 55. 1601.

Syringa suaveolens Moench, Meth. 678. 1794.

Philadelphus salzmanni Hort. ex Koch, Dendrol. 1: 338. 1869, *nom. nud.*, in syn.

Philadelphus kochianus Koehne, Deutsche Dendr. 183. 1893.

Philadelphus triflorus Hort. ex Nicholson in Kew Hand-List 1: 225. 1894, non Wall.

Philadelphus coronarius var. *vulgaris* Schrad. ex DC., Prodr. 3: 205. 1828.— Loudon, Arb. Frut. Brit. 2: 951. 1838.

Philadelphus aromaticus Hort. ex Steud. Nom. 611. 1840.

Philadelphus coronarius var. *genuinus* Maxim. in Mém. Acad. Sci. St. Pétersb. VII. 10 (16): 37 (Rev. Hydrang. As. Or.). 1867.— Franch. & Sav., Enum. Pl. Jap. 1: 56. 1873.

Philadelphus deyrolleanus Lavallée, Arb. Segrez. Enum. 116. 1877.

Philadelphus kochianus Koehne, Deutsche Dendr. 188. 1893.

Philadelphus pallidus Hayek ex Schneider, Ill. Handb. Laubh. 1: 373, fig. 237, x-z; 238, h-k. 1905.— Hayek, Fl. Steierm. 1: 725. 1909.— Hegi, Ill. Fl. Mittel.-Eur. IV. 2: 641. 1922.— Prodan, Fl. Determ. Descr. Pl. Rômania 1: pl. 8, fig. 88. 1923.— Engler, Pflanzenf. ed. 2, 18a: 192. 1930.— Sata, Ill. Manch. Mong. Trees ed. 2, 127, fig. 90. 1943.

Philadelphus zeyheri var. *kochianus* (Koehne) Rehder in Jour. Arnold Arb. 1: 201. 1920; Man. Cult. Trees Shrubs 277. 1927; ed. 2, 272. 1940; et Bibl. Cult. Trees Shrubs 194. 1949.

TYPE: Linnaean Herbarium No. 634.1.

An upright, rather stiff shrub with some arching branches, the second year's growth moderately exfoliate, the current year's growth brown, sparsely pubescent or glabrescent. Leaves ovate, 4.5–9 cm. long, 2–4.5 cm. wide, subglabrous, pubescent on the primary nerves and nerve-angles beneath; subdenticate with 6 to 11 teeth on each side, obtuse or acute at the base, 3- or 5-nerved, acuminate at the apex. Flowers fragrant, the inflorescence a determinate raceme, 5- to 9-flowered, more on vigorous twigs or less on weak ones, the last pair usually in the axils of normal leaves, sometimes cymose; hypanthia glabrous with few hairs at the base merging into the sparsely pubescent pedicel; at anthesis the pedicels 6–10 mm. long, in fruit 6–20 mm. long; sepals ovate, 4–5 mm. long, glabrous; corolla subdisciform, 2.5–3 cm. across, the petals obovate, 12–14 mm. long, 11 mm. wide, the apex rounded; stamens ca. 25; disc and style glabrous,

the adaxial stigmatic surface three times longer than the abaxial. Capsules turbinate, 6–8 mm. long, 5–6 mm. in diameter, the persistent calyx subapical. Seed spindle-shaped, 3 mm. long, 0.75 mm. wide, the testa brown, slightly striate, the slender tail as long as the minute embryo.

AUSTRIA: Wien, *Handel-Mazzetti* on June 16, 1935 (A).

CAUCASUS: Borjom, *C. S. Sargent*, July 19, 1903 (A); Kuban, *N. Busch & P. Klopotow*, May 1907 (A).

CULTIVATED: Europe: Upsala, Linnaean Herb. 634.1 (photo of TYPE, A). Hort. Göttingen, *A. Rehder* 1612, 1614, 1635, 1641, 1670, 2230 (all at A); Hanover, Botanischer Garten der Forstakademie, *H. Zabel* in 1873 (A). Hort. Simon Louis, Plantière, *C. K. Schneider* in 1906 (A). United States: Arnold Arboretum 4785-1 (A).

Philadelphus coronarius Linn. is the type species of the genus. It is also the most widely cultivated and the best known species of the genus. Written accounts about it can be found in almost all languages existing in the northern hemisphere. The relatively large number of references cited above represent only a selection from the more important literature regarding it. It has been associated with man since time immemorial, and its nativity is now obscure. Thus botanists have no agreement regarding its origin. Modern horticulturists and taxonomists like Bean of Kew and Rehder of the Arnold Arboretum consider it a native of southern Europe, from Italy to the Caucasus. I have not been able to find any statement to this effect in the floras of these regions. As early as the sixteenth century Clusius observed its occurrence in Spain, Austria and Hungary, remarking at the time that it had never been found in a wild state in those countries. He thought that it might have been first cultivated in Belgium. When Linnaeus established the species he doubtfully assigned its origin to Verona. Schrader in 1838 gave a negative statement as to the possibility of its spontaneous occurrence in southern Germany and Bohemia and suggested that it had probably been introduced from the Orient, possibly from Japan. Boissier in his *Flora Orientalis* maintained that it was not truly spontaneous in the area covered. As to the countries of southern Europe, I have not been able to find in the published floras of Italy, Spain, or Portugal any statement about its spontaneous occurrence in those countries.

Morphologically this species has the seed character of the Japanese element, the leaf and style characters of the Amur River element. In spite of the relative geographical proximity, its relationship with the Himalayan element is rather remote.

In early botanical literature there are two elements ascribed to *P. coronarius*. One is the material typified by the specimen in the Linnaean herbarium, and the other is represented by the plate in *Bot. Mag.* 11: pl. 391. 1797. The leaves of the plant pictured in this plate have coarser teeth, acute sepals, and elliptic petals. It suggests *P. lewisii* Pursh rather than the Linnaean species.

Cultivation has apparently proved that *P. coronarius* Linn. is a heterogeneous species. Through special care growers have segregated and prop-

agated many garden varieties which appear completely different from the typical form. Some of these forms are compact and dwarf, while others are stiff and rather loose in habit. Nearly all of them have short, depauperate inflorescences. Some of them are shy to flower, and some others rarely flower — for example, Dippel observed a twenty-year-old dwarf form which had never flowered. Many have double flowers. Some of them have been treated as putative hybrid species by some authors and forms or varieties of *P. coronarius* Linn. by others. As none of them occurs in the wild state, they are treated as garden varieties here.

KEY TO THE VARIETIES OF *P. coronarius*

- A. Leaves uniformly green.
- B. Low compact shrubs up to 1 meter high.
- C. Leaves opposite, 2 at each node.
 - D. Pedicels villose. a. var. *duplex*.
 - DD. Pedicels glabrous.
 - E. Flowers highly doubled, the petals pointed at the apex. b. var. *deutziaeflorus*.
 - EE. Flowers semi-doubled, the petals rounded at the apex. c. var. *dianthiflorus*.
- CC. Leaves verticillate, 3 at each node. d. var. *cochleatus*.
- BB. Tall shrubs over 2 m. high, the branchlets stiff and loose, rarely drooping; leaves ovate, ovate-elliptic, or elliptic.
 - C. Flowers simple. e. var. *zeyheri*.
 - CC. Flowers doubled. f. var. *primulaeflorus*.
- AA. Leaves variegated. g. var. *variegatus*.

29a. *Philadelphus coronarius* Linn. var. *duplex* West., Univ. Bot. 1: 205. 1770.—Rehder, Man. Cult. Trees Shrubs 277. 1927; ed. 2. 271. 1940.—Chen, Ill. Man. Chin. Trees Shrubs 375. 1937.

Philadelphus nanus Mill., Gard. Dict. ed. 8, 34. 1768.

Philadelphus coronarius Linn. var. *nanus* Aiton, Hort. Kew. 2: 155. 1789.—DC., Prodr. 3: 205. 1828.—Schrader in Linnaea 12: 390. 1838.—Anon. in Gard. 40: 289. 1891.—Dippel, Handb. Laubh. 3: 337. 1893.—Voss, Vilmor. Blumengärt. 1: 290. 1894.—Bean, Trees Shrubs ed. 7, 2: 412. 1950.

Philadelphus coronarius *nanus* Granz Schmidt, Oester. Allg. Baumz. 1: 57, t. 60. 1792.

Philadelphus coronarius var. *flore plena* Loddiges ex Loudon, Arb. Brit. 2: 951. 1838.—Anon. in Garden 40: 289. 1891.

Philadelphus coronarius Linn. var. *pumilus* West., Univ. Bot. 205. 1770.—Rehder, Man. Cult. Trees Shrubs 277. 1927; ed. 2, 271. 1940.—Chen, Ill. Man. Chin. Trees Shrubs 375. 1937.

Philadelphus coronarius Linn. forma *pumilus* (West.) Rehder, Bibl. Cult. Trees Shrubs 193. 1949.

LECTOTYPE: Kew, G. Nicholson 1307 (A).

Dwarf shrubs, the branchlets castaneous, the bark of the second year's growth exfoliating, the current year's growth villose, the hairs compressed,

the leaves oblong-elliptic, 3–5 cm. long, 1–2.5 cm. wide, inconspicuously villose on both surfaces, serrate, those on the virgin shoots broad ovate, 6–8 cm. long, 4–4.5 cm. wide, abruptly acuminate, coarse dentate, uniformly villose, the hairs ± erect; flowers doubled, ternate or in depauperate 5-flowered, rarely 7-flowered racemes with the lower ones in the axils of normal leaves, the pedicels 2–3 mm. long, villose; the hypanthium and calyx glabrous or glabrescent; corolla 2.5 cm. across, the petals oblong, rounded at the apex.

ENGLAND: Kew, *G. Nicholson* 1307 (A), 2597 (A).

GERMANY: Hort. Göttingen, *A. Rehder* 1606 (A).

AUSTRIA: *Henric Braun*, May 15, 1907 (A); *Handel-Mazzetti*, June 16, 1935 (A).

UNITED STATES: Massachusetts: Cambridge Bot. Gard., June 3, 1880 (A); Arnold Arboretum field no. 2784 (A). California: Univ. of California Bot. Gard. no. 3434.

This variety probably originated in the gardens of England, where it has been known as *nanus*. Rehder, in his Manual of Cultivated Trees and Shrubs, recognized two varieties, *duplex* and *pumilus*, both of which have *nanus* as a synonym. Although he gave no reason for this separation, one judges, from the material he worked with, that he named the flowering specimen *duplex* and the non-flowering specimens *pumilus*. The British *nanus* is well known for its tardiness in flowering. Dippel recorded one case where the plant was twenty years old and had never flowered. I have examined both the flowering and the sterile specimens with a microscope to see if there may be a difference in the type of hairs present on the branchlets and leaves. I see no reason for keeping *duplex* and *pumilus* as distinct varieties. As *duplex* is the older varietal name, it should be the valid name for this variety. It can be recognized by its dwarf habit, pubescent branchlets and leaves, tardiness and paucity in flowering, double flowers with glabrous hypanthia and calyces, and its rounded petals.

29b. *Philadelphus coronarius* Linn. var. *deutziaeeflorus* Hartwig, Ill. Gehölz. 258. 1892. — Schelle in Beissner & al., Handb. Laubh.-Ben. 128. 1903. — Rehder, Man. Cult. Trees Shrubs 277. 1927; ed. 2, 271. 1940.

Philadelphus coronarius Linn. forma *deutziaeeflorus* (Hartwig) Rehder in Jour. Arnold Arb. 1: 201. 1919; et Bibl. Cult. Trees Shrubs 193. 1949.

Philadelphus coronarius Linn. var. *multiflorus plenus* Rehder in Bailey, Cycl. Am. Hort. 3: 1298. 1901, *nom. nud.*

LECTOTYPE: Arnold Arboretum 5852, *A. Rehder*, June 23, 1920 (A).

A low compact shrub, the branchlets castaneous, the bark of the second year's growth exfoliating, the current year's growth glabrous, the newly growing vegetative shoots inconspicuously pilose; leaves ovate, 2–5 cm. long, 1.5–2.5 cm. wide, glabrous on both surfaces, occasionally inconspicuously pilose on the principal nerves, subentire or finely serrate at the

apical end, those on the vegetative shoots up to 9 cm. long, 6 cm. wide, glabrous except on the principal nerves and nerve-angles beneath; flowers doubled, in 3's, or in depauperate 5-flowered racemes, the pedicels glabrous. 7-10 mm. long; hypanthium and calyx glabrous; corolla 3 cm. across, the petals more or less pointed at the apex.

UNITED STATES: Arnold Arboretum 5852, without collector, June 21, 1916 (A); *A. Rehder*, June 23, 1920 (A, LECTOTYPE).

This variety probably originated in the Späth Nursery at Berlin.

29c. *Philadelphus coronarius* var. *dianthiflorus* Dippel, Handb. Laubh. 3: 337. 1893.—Rehder in Bailey, Cycl. Am. Hort. [3]: 1298. 1901.—Bean, Trees Shrubs 2: 133. 1914, ed. 7, 2: 412. 1950. et in Chitt., Dict. Gard. 3: 1546. 1951.

LECTOTYPE: Arnold Arboretum 2222-1, *A. Rehder*, June 23, 1920 (A).

A dwarf shrub with arching branchlets, the second year's growth gray, with close but tardily wearing off bark, the current year's growth glabrescent; leaves oblong-ovate, very weakly denticulate, 1.5-5.5 cm. long, 1-3.5 cm. wide, obtuse or rounded at the base, short and abruptly acuminate at the apex, glabrescent on both surfaces, those on the vegetative shoots up to 9 cm. long, 6 cm. wide, sparsely strigose-villoso beneath; flowers in 3's, solitary or 5 in short determinate racemes, the pedicels, hypanthia and calyces glabrous; the corolla semidoubled, the petals rounded at the apex.

GERMANY: Botanischer Garten der Forstakademie, Hannover, *H. Zabel*, June 13, 1894.

UNITED STATES: Arnold Arboretum, *A. Rehder*, June 23, 1920.

This variety appeared first in German literature. It probably originated in that country. The above-cited Zabel collection represents the oldest specimen of this form that I have examined. This specimen records that as early as 1889 it was ready for distribution in the Späth nursery at Berlin. It is closely related to *P. coronarius* var. *primulaeflorus*. It can be readily distinguished from the latter variety by its dwarf habit, semidouble flowers, and glabrous pedicels. It is also closely related to *P. coronarius* var. *deutziaeeflorus*. The latter variety has highly doubled flowers with pointed petals and more sharply serrate leaves.

29d. *Philadelphus coronarius* Linn. var. *cochleatus* Lavallée, Arb. Segrez. Enum. 114. 1877, *nom. nud.*

LECTOTYPE: *C. Schneider*, Sept. 1903 (A).

A low shrub, the branchlets glabrous, leaves 3 at a node, verticillate, broad-elliptic, 2-2.5 cm. long, 1-2 cm. wide, obtuse at both ends, subentire, with 2 or 3 minute, inconspicuous teeth on each side, glabrescent above, hirsute on the principal nerves beneath. The flowers not known.

FRANCE: Plantières, Herb. Dendr. Schneider, Sept. 1903 (A).

I have not been able to locate the valid publication of this trinomial. It apparently originated in France and has not been popular among growers. The only specimen that I have seen is sterile. The lower three pairs of leaves of this specimen are opposite, and the upper ones are verticillate, three at each node. Although there is no flower, I do not doubt its identity as a *Philadelphus*, and I think it is a distinct variety.

29e. *Philadelphus coronarius* var. *zeyheri* (Schrader) Hartwig & Rümpler, Baume Sträuch 391. 1875.

Philadelphus zeyheri Schrader ex DC., Prodr. 3: 205. 1828; et in Linnaea 12: 390. 1838.—Loudon, Arb. Frut. Brit. 2: 952. 1838.—Lavallée, Arb. Segrez. Enum. 115. 1877.—Rehder, Man. Cult. Trees Shrubs 277. 1927, ed. 2, 271. 1940; et Bibl. Cult. Trees Shrubs 191. 1949.—Bean, Trees Shrubs ed. 7, 2: 420. 1950; et in Chitt., Dict. Gard. 3: 1547. 1951.

TYPE: Cultivated, *Schrader*, 1827 (Genève).

An erect shrub up to 2 m. high, the bark of the second year's growth castaneous, exfoliate, the current year's growth sparsely pilose; leaves ovate, those on the vegetative shoot 6–10 cm. long, 3–6 cm. wide, those on the flowering shoot 4–5 cm. long, 2.5–3.5 cm. wide, rounded or obtuse at the base, acuminate at the apex, serrate, glabrous above, sparsely pilose on the nerves beneath; inflorescences 3- or 5-flowered; when 5, the lower pair in the axils of normal or diminuted and lanceolate leaves; hypanthia glabrous; sepals ovate, 5 mm. long, 3 mm. wide at the base; corolla disciform, 2.5–3 cm. across, the petals suborbicular, 1–1.5 cm. in diameter; stamens ca. 32; disc and style glabrous, the stigma clavate, the adaxial surfaces 4–6 times longer than the abaxial; capsules turbinate, 7 cm. long, 6 cm. in diameter.

CULTIVATED: Europe: Kew, G. Nicholson 1318 (A), 1319 (A); Conservatoire et Jardin botaniques, *Schrader*, 1827 (Genève, TYPE; photo A); Bot. Gart. Forstakadamie, Hannover 6, H. Zabel, June 17, 1873 (A), Sept. 1, 1873 (A); Wien, N. Braun in 1907 (A). United States: Arnold Arboretum 5881-1 = 15425, without collector, June 30, 1913 (A), Sept. 10, 1913 (A), June 13, 1914 (A); 7872, A. Rehder, July 18, 1918 (A), June 19, 1919 (A).

When Schrader published *P. zeyheri* he accredited the taxon to American origin. As its wild equivalent is not known in the New World, and as its exfoliation of the bark and dentation of the leaves match best with *P. coronarius* Linn., it is thus treated as a cultivar of this species. Rehder treated it as a putative hybrid between *P. coronarius* and *P. inodorus* or *P. grandiflorus*. Part of his material has pubescent discs. When those specimens are taken out, the rest fit well as a variety of *P. coronarius* Linn. What Rehder considered as \times *P. zeyheri* var. *kochianus* is a normal *P. coronarius* Linn.

29f. *Philadelphus coronarius* [var.] *primulaeflorus* [Carr.] T. Moore in Flor. Pom. 1873: 182, fig. 1873.—Rehder, Man. Cult. Trees

Shrubs 277. 1927; ed. 2, 271. 1940.—Chen, Ill. Man. Chin. Trees Shrubs 375. 1937.

Philadelphus primulaeflorus Carr. Rev. Hort. 1870: 305, fig. 47. 1871.—Anon. in Gard. Chron. 1871: 5. 1871.—T. Moore, l.c.

Philadelphus coronarius forma *primulaeflorus* Nicholson, Ill. Dict. Gard. 3: 94, fig. 106. 1887.—Schelle in Beissner & al., Handb. Laubh.-Ben. 128. 1903.—Rehder, Bibl. Cult. Trees Shrubs 193. 1949.

Philadelphus coronarius var. *primulaeflorus plenus* Hartwig, Ill. Gehölzb. 258. 1892.

Philadelphus coronarius var. *rosaeflorus plenus* Hort. ex Hartwig, l.c.—Moore in Bailey, Stand. Cycl. Hort. 5: 258. 1916, in syn.

Philadelphus ketuleeri Hort. ex Dippel, Handb. Laubh. 3: 337. 1893, in syn.

Philadelphus coronarius var. *multiflorus plenus* Hort. ex Rehder in Bailey, Cycl. Am. Hort. [3]: 1298. 1901, nom. nud.—Moore in Bailey, Stand. Cycl. Hort. 5: 2580. 1916.

Philadelphus coronarius var. *plenus* Bean, Trees Shrubs ed. 7, 2: 412. 1950.

LECTOTYPE: Arnold Arboretum 6600, *A. Rehder*, June 19, 1919.

A compact tall shrub up to 2 m. high, with arching branchlets, the second year's growth castaneous, the bark exfoliating, the current year's growth sparsely but verrucosely villose, the hairs with thickened bases; leaves broad-ovate, 3–7 cm. long, 2–4 cm. wide, those on the vegetative shoots up to 9 cm. long, 7 cm. wide, rounded at the base, abruptly short-acuminate at the apex, sparsely pilose along the nerves above, strigose-villose beneath; flowers in 2's or 3's, solitary, or five in a crowded determinate raceme with the lower pair in the axils of normal leaves, the pedicels 4–8 mm. long, sparsely but uniformly villose, the hairs erect, ± compressed; hypanthium glabrous, with a few hairs at the base or on the angles; calyx glabrous, broad-ovate, 6 mm. long, 3–4.5 mm. wide, acuminate at the apex; corolla 3–3.5 cm. across, with doubled petals; stamens generally sterile, with various modifications. Fruit obconic; seeds generally not fertile, with relatively short tails.

CULTIVATED: United States: Arnold Arboretum: *A. Rehder*, July 18, 1918 (A), June 19, 1919 (A); *E. J. Palmer*, June 11, 1936 (A).

This variety is of garden origin. Obviously it is a hybrid with unknown pedigree. Carrière, who first observed it in a French garden, interpreted it as a species. He did not give its history or establish its affinity. Two years later T. Moore summarized Carrière's account in English and reproduced the original illustration under the name *P. coronarius primulaeflorus*. He failed to give a definite rank to this trinomial, which I interpret as a variety. The subentire broad-ovate leaves and the relatively small number of flowers in each inflorescence, and the large sepals, suggest some relation with *P. inodorus* Linn. Based on obvious morphological characters, it is legitimate to assume it to be a hybrid between *P. coronarius* Linn. and *P. inodorus* Linn. According to available records this variety was introduced in America through the Arnold Arboretum in November 1908, under the field number 6600. The Späth Nursery in Berlin was then its distributor.

29g. *Philadelphus coronarius* Linn. var. *variegatus* Weston, Univ. Bot. 1: 205. 1770.—Lodd., Cat. 25. 1823.—Loudon, Arb. Frut. Brit. 2: 951. 1838.—Anon. in Garden 40: 209. 1891.—Chen, Ill. Man. Chin. Trees Shrubs 375. 1937.—Bean, Trees Shrubs 2: 134. 1914; ed. 7, 412. 1950.

Philadelphus coloratus Dippel, Handb. Laubh. 3: 338. 1893, pro parte.

Philadelphus coronarius forma *variegatus* (West.) Schelle in Beissner & al., Handb. Laubh.-Ben. 128. 1903.—Rehder, Cult. Trees Shrubs ed. 2, 271. 1940; et Bibl. Cult. Trees Shrubs 193. 1949.

Philadelphus coronarius Linn. fol. *argenteo-marginatis* Hort. ex Dippel, l.c., in syn.—Moore in Bailey, Stand. Cycl. Hort. 5: 2580. 1916.

LECTOTYPE: Hort. Parkman, June 19, 1881 (A).

A sickly-looking dwarf shrub, the second year's growth gray, the bark closed, tardily wearing off, the current year's growth sparsely villose; leaves ovate, ± deformed, 2–3 cm. long, 1.5–2 cm. wide, white at the margin, rounded at the base, acute at the apex, glabrous or glabrescent above, sparsely villose, especially on the nerves beneath; flowers in 3- or 5-flowered depauperate racemes, the pedicels 2–6 mm. long, villose; hypanthium and calyx glabrous or glabrescent; corolla disciform, 2.5 cm. across, the petals suborbicular, 10 mm. in diameter; stamens ca. 25, many anthers appearing sterile; disc and style glabrous, the style 5 mm. long, divided almost to the base.

CULTIVATED: United States: Hort. Parkman, June 19, 1881 (A).

This variety was known to growers in England as early as 1770. There is no record about its origin. It is very likely a sport of *P. coronarius*. Although the standard manuals or encyclopedias of American horticulture all devote a line to this plant, it is extremely rare in American gardens. The above cited specimen is the only one that I have seen.

30. *Philadelphus caucasicus* Koehne in Gartenfl. 45: 619. 1896; et in Mitt. Deutsche Dendr. Ges. 1904 (13): 85. 1904.—Schneider, Ill. Handb. Laubh. 1: 374. 1905.—Poiarkova in Komarov, Fl. URSS 9: 220. 1939.

TYPE MATERIAL: Abchasien, *Karpinsky*; Kuban, *Kusnetzoff*; Pontische Region, *Kusnetzoff*.

An upright shrub with some arching branches, the second year's branchlets light brown, exfoliate, the current year's growth brown, weakly villose. Leaves elliptic or ovate-elliptic, 5–9 cm. long, 2–3, rarely up to 4 cm. wide, obtuse or acute at the base, 5- rarely 3-nerved, abruptly short-acuminate at the apex, subentire or very faintly and remotely serrulate, each side with 0 to 8 teeth, glabrous or glabrescent above, uniformly pubescent beneath, the hair villose. Flowers in determinate racemes, 5- to 9-flowered, the pedicels 3–10 mm. long, weakly villose; hypanthium and calyx weakly loose villose, the hair slightly crisp; sepals ovate, 5–6 mm. long, 3.5 mm. wide; corolla subdisciform, 3 cm. across, the petals obovate, 1.3 cm. long,

1 cm. wide, stamens ca. 22, the longest 6 mm. long, disk and style densely yellow villose, the style 6 mm. long, the upper one-third divided, the stigma clavate, the adaxial surface on a narrow ridge, twice as long as the abaxial. Capsules turbinate, 6–7 mm. long, 5–8 mm. across the top, the persistent sepals apical. Seed rather plump, short-caudate, the embryo ca. 1.25 mm. long, 0.75 mm. wide, the tail half as long as the embryo, often obtuse, the crown with rounded lobes.

EUROPE: Russia: Kutais, *A. Lomoikin*, May 1922 (A). Transcaucasia: Azerbajdzhan, distr. Zakataly, *I. Beidemann*, July 21, 1935 (A).

Koehne proposed this species on the basis of three collections, not designating any one as the type. As these materials are not available to me, the identification of this species is made on the basis of his description. Accordingly, the specimens with uniformly pubescent lower leaf-surfaces, weakly pubescent hypanthia and sepals, and pubescent disc and style are interpreted as the typical *P. caucasicus* Koehne.

The Caucasian material that I have examined demonstrates an obvious difference in the density of the hairs on the hypanthia and styles. Some plants apparently have glabrous hypanthia and styles. The fruiting specimens of these plants also have glabrous lower leaf-surfaces. In this respect they approach *P. coronarius* Linn. Nevertheless they can be distinguished from the latter species by their pubescent discs. The plants cultivated in outstanding American botanical gardens are this glabrous form. That in the Arnold Arboretum, numbered 21326-B, exhibits variations in the sizes of the leaves and flowers. On a vigorously growing branchlet the leaves are 6 cm. long and 3 cm. wide, and the petals are 12 mm. wide. On a weak branchlet of the same plant the leaves are only 3 cm. long, 1.3 cm. wide, and the petals are 8 mm. wide. The indumentum on the large and small leaves and flowers is the same. This observation seems to prove that the pattern of the indumentum of the individual plants in this group is a rather stable character. Thus I think the glabrous form is distinct enough to warrant a varietal name.

There is a yellow-leaved old garden form which has been assigned as a variety of *P. coronarius* in standard manuals dealing with trees and shrubs for the last half-century. An examination of the specimens at hand, sent to the Arnold Arboretum from various botanical gardens, reveals that they all have pubescent styles and discs. Thus a transfer is necessary.

KEY TO THE VARIETIES OF *P. caucasicus*

A. Tall mound-shaped shrub up to 2.5 m. high; leaves green; hypanthia very sparsely pilose or glabrous. a. var. *glabratus*.
AA. Low shrub 1–1.5 m. high; leaves yellow; hypanthia uniformly sparsely villose. b. var. *aureus*.

30a. *Philadelphus caucasicus* var. *glabratus*, var. nov.

Philadelphus caucasicus sensu Rehder, Man. Cult. Trees Shrubs ed. 2, 271. 1940; et Bibl. Cult. Trees Shrubs 193. 1949, non Koehne.

Frutex 2-2.5 m. altus, ramis griseis, bienniis castaneis, exfoliatis, hornotinis sparse villosis; foliis ellipticis vel ovato-ellipticis, 3-7 cm. longis, 1.5-3 cm. (raro usque ad 4 cm.) latis, basi acutis, obtusis, raro rotundatis, apice breviter acuminatis, supra glabris vel glabrescentibus, raro sparse strigoso-villosis; inflorescentiis racemosis, 7- usque ad 11-floribus; pedicellis, hypanthiis et calycibus glabris, disco villoso, stylo glabro.

EUROPE: Caucasus: Tiflis, S. Michajlowsky, Sept. 1903 (A); Kutais, A. Lomoikin, May 1922 (A); Kuban, V. J. Vorobjew & B. N. Klopotow, July 1, 1906 (A, TYPE); same locality, N. Busch & B. Klopotow, May 11, 1907 (A).

CULTIVATED: Europe: Hort. Göttingen, A. Rehder 1609 (A), 1637 (A); Hort. Müskau, A. Rehder, July 1888 (A); Bot. Gart. Forstakadamie 15, H. Zabel, June 17, 1873 (A). United States: Arnold Arboretum 6964, without collector, June 13, 1914 (A); 21703-A, E. J. Palmer, June 6, 1936 (A); 21703-B, E. J. Palmer, June 18, 1940 (A), S. Y. Hu, June 8, 1951 (A); 22482, E. J. Palmer, June 10, 1927 (A); 948-27, C. E. Kobuski & C. K. Allen in 1933 (A).

The genuine *P. caucasicus* Koehne has not been known in cultivation. The plants introduced into American gardens from the Caucasus belong to this variety. Arnold Arboretum 21707-A is raised from seed obtained from the Botanical Garden at Tiflis, and 21326-B came from the Boyce Thompson Institute, Yonkers, N. Y.

30b. *Philadelphus caucasicus* var. *aureus* (Rehder), comb. nov.

Philadelphus coronarius var. *aureus* Hort. ex Rehder in Bailey, Cycl. Am. Hort. [3]: 1298. 1901.

Philadelphus coronarius var. *fol. aureis* Hartwig, Ill. Gehölzb. 259. 1892.

Philadelphus coronarius forma *aureus* Hort. ex Schelle in Beissner et al., Handb. Laubh.-Ben. 128. 1903.

LECTOTYPE: Arnold Arboretum 5953, without collector, June 11, 1914 (A).

A sickly-looking shrub, 1.5 m. tall, the bark of the second year's growth castaneous, exfoliating, the current year's growth sparsely villose; leaves ovate, 3-5 cm. long, 1.5-3 cm. wide, obtuse or rounded at the base, shortly acuminate at the apex, yellow-green, prominently serrate, glabrous above, strigose-pilose on the principal nerves and in their angles; inflorescences 5-, 7-, rarely 3- or 9-flowered, the hypanthia with few hairs at the base, the sepals glabrous, ovate, 5 mm. long, 3-4 mm. wide; corolla disciform, 2.5 cm. across, the petals oblong-suborbicular, 11 mm. long, 10 mm. wide, the apex rounded; stamens ca. 22; disc hirtellous, style glabrous, the stigma clavate.

CULTIVATED: Europe: Kew, G. Nicholson 1006 (A); Breslau, Scheitniger Park, C. Baenitz, June 20, 1905 (A). United States: Arnold Arboretum 5953, without collector, June 11, 1914 (A, LECTOTYPE).

This is a rare variety. I have seen it only once, on Rockview Street, Jamaica Plain, Mass.

31. *Philadelphus salicifolius* Koch, Dendr. 1: 337. 1869.

Philadelphus coronarius var. *salicifolius* (Koch) Jäger, Ziergeh. ed. 2, 236. 1884.
 — Dippel, Handb. Laubh. 3: 337. 1893. — Schneider, Ill. Handb. Laubh. 1: 374. 1905. — Rehder, Man. Cult. Trees Shrubs 277. 1927; ed. 2, 271. 1940. — Chen, Ill. Man. Chin. Trees Shrubs 375. 1937. — Bean, Trees Shrubs ed. 7, 2: 412. 1950.

Philadelphus coronarius forma *salicifolius* (Koch) Voss, Vilmor. Blumengärt. 1: 290. 1894. — Rehder, Bibl. Cult. Trees Shrubs 193. 1949.

LECTOTYPE: Arnold Arboretum 18070, S. Y. Hu, June 14, 1951 (A).

A dwarf compact shrub up to 1 m. high, the second year's growth castaneous, the bark exfoliate, the current year's growth glabrous or glabrescent. Leaves lanceolate, those on the flowering shoot 3.5–7 cm. long, 1–1.5 cm. wide, acuminate at both ends, glabrous on both surfaces, rarely with few weak hairs on the principal nerves beneath, remotely and inconspicuously serrulate, those on the vegetative shoots 8–13 cm. long, 2–3 cm. wide, occasionally ovate on abnormal off-shoots, 7–8 cm. long, 5–6 cm. wide, acute or rounded at the base, acuminate at the apex. Flowers ternate, solitary or on depauperate racemes, the pedicels 2–4 mm. long, glabrous or sparsely villose, the hypanthium and calyx glabrous; sepals ovate-lanceolate, 5–6 mm. long, 2 mm. wide at the base; corolla stellate, 2–3 cm. across, the petals oblong-lanceolate, 1.2–1.4 mm. long, 5 mm. wide, the apex acutish, hirtellous; stamens ca. 21, the rim of the disc pubescent, style 5 mm. long, glabrous, divided almost to the base, the stigmas clavate, the abaxial surface half as long as the adaxial.

CULTIVATED: Europe: Bot. Gart. Forstakademie, Hannover, H. Zabel 27 (A); Hort. Bot. Leipzig, C. K. Schneider, June 26, 1904 (A); Hort. Simon Louis, Plantières, C. K. Schneider, June 25, 1906 (A). United States: Arnold Arboretum field no. 5875, E. J. Palmer, May 11, 1936 (A); without collector, June 21, 1916 (A); 18070, June 21, 1927 (A); S. Y. Hu, June 14, 1951 (A, LECTOTYPE).

This distinctive taxon probably originated in Germany. Koch recorded its existence as early as 1869. In the last three quarters of a century, botanists and horticulturists were inclined to interpret it as a variety or a form of *P. coronarius* Linn. This is probably due to the fact that suckers with broad-ovate *coronarius*-type of leaves often shoot from a normal dwarf *salicifolius* plant. Nevertheless, the distinctiveness of this taxon does not lie in its leaf-form. Its depauperate inflorescences, stellate corolla, oblong-lanceolate petals hirtellous at the apex, its small number of stamens, its much divided style, and its pubescent disc are of sufficient distinction to warrant specific rank. Its relationship seems to be closer to *P. caucasicus* Koehne than to *P. coronarius* Linn. Although this species has been known for almost a century, its distribution is very limited. So far as I know it exists only in a few botanical gardens. This lack of popularity among growers is probably due to its shy-flowering nature. It came to America in 1908 through the Arnold Arboretum, where it has been propagated by cuttings. Späth Nursery at Berlin, if not the originator, has been the chief distributor of this species.

(To be continued)

INDUCTION OF EARLY FLOWERING OF ORNAMENTAL APPLE TREES

KARL SAX AND ALBERT G. JOHNSON

HORTICULTURISTS have long known that the time of flowering of fruit trees could be hastened by various treatments which inhibit vegetative growth. The blocking of phloem transport from the leaves to the root system has been effected by girdling the trunk of the tree, by grafting on dwarfing rootstocks, or, more recently, by inverting a ring of bark on the trunk of the tree (6). Root pruning or confining the root system in pots also inhibits vegetative growth and promotes flowering. Pot binding has long been used to produce dwarf ornamental trees in Japan, and European foresters have used root pruning to promote early seed production in tree-breeding experiments. The bending of branches in a horizontal position also promotes early fruiting and is the basis for the "Spindlebush" method of training fruit trees in Europe.

The general relationship between growth of trees and the production of flowers and fruits was described by Thomas Andrew Knight (2) as follows: "According to that hypothesis, the true sap of trees is wholly generated in their leaves, from which it descends through their bark to the extremities of their roots, depositing in its course the matter which is successively added to the tree; whilst whatever portion of such sap is not thus expended sinks into the alburnum, and joins the ascending current, to which it communicates powers, not possessed by the recently absorbed fluid. When the course of descending current is intercepted, that necessarily stagnates, and accumulates above the decorticated space; whence it is repulsed, and carried upward, to be expended in an increased production of blossoms, and of fruit. . . . The repulsion of the descending fluid therefore accounts, I conceive satisfactorily, for the increased production of blossoms, and more rapid growth of the fruit upon the decorticated branch." Radioactive tracer tests and chemical analyses of the leaves of dwarfed trees done by graduate students at the Bussey Institution confirm Knight's observations made nearly 140 years ago.

The various methods for promoting earlier flowering and fruiting appear to be related to auxin formation and nutritional balance. The suppression of auxin production or accumulation associated with decreased vegetative growth is generally related to precocious flower and fruit production (1). Nutritional balance also appears to be involved in the production of flower buds. According to Klebs a high ratio of carbohydrates to nitrogen and mineral nutrients promotes flowering (3). This conclusion was supported by the later work of Kraus and Kraybill. More recently Roberts (4) found that flowering of shaded *Xanthium* plants could be hastened by spraying the leaves daily with a sugar solution. Although there is considerable evi-

dence in support of the control of flowering by the carbohydrate-nitrogen ratio, the relationship does not appear to be a simple one (1).

Precocious flowering of apple trees may also be promoted by the physiological incompatibility between the rootstock and the grafted scion variety. Certain rootstock varieties greatly inhibit the growth of the bud or scion of certain horticultural varieties of apples, but if the rootstock variety is used as an interstock on a compatible rootstock the dwarfing effect is greatly reduced. In these cases the dwarfing effect is not due to a poor graft union or to the checking of phloem transport through the dwarfing rootstock stem, but is caused by the interaction between the root system and the scion variety (5).

There is also some evidence that flowering may be induced by a "flowering hormone." This idea was first proposed by Sachs. In 1883 he found that cuttings taken from flowering begonias bloomed much earlier than cuttings taken from plants which had not bloomed. Vöchting grafted adventitious buds of beets into one- and two-year-old roots. The buds on the one-year-old roots produced only vegetative shoots, but those on two-year-old roots produced flowering stems. Cuttings or scions from old trees will usually flower earlier than those from immature trees (3). The grafting of scions from young seedlings on mature fruiting trees to hasten flowering and fruiting of the seedling variety may involve the transmission of a "flowering hormone" from stock to scion, since this method of inducing earlier flowering is not related to the suppression of vegetative growth. Similar evidence for the transmission of a flowering-inducing substance is found in grafts of certain herbaceous plants. Long-day non-flowering plants were induced to flower, even under the influence of long days, by grafting on them short-day variety scions bearing flower buds (1). Although no specific plant substance has been isolated which will stimulate flowering, there is considerable indirect evidence to support Sachs' theory that flowering may be induced by a specific hormone which is formed or accumulated by various internal and external factors.

Experiments with an apomictic variety of ornamental apple variety seem to support the concept of a "flowering hormone." The apple variety used was a hybrid between *Malus Sargentii* and *M. astracanica* designated by the planting number 33340. *Malus Sargentii* when open pollinated is completely apomictic and breeds true from seed. When artificially pollinated with pollen of certain species it does produce some sexual hybrids. The hybrid 33340, like the mother parent, is also apomictic and breeds true from seed. The original hybrid first flowered at the age of six years, and its apomictic seedlings produce flowers at about the same age. Since the hybrid is apomictic it is possible to test the fruiting response of old and young seedling trees which are of identical genetic constitution.

An attempt to induce early flowering by grafting scions from the young one-year-old seedlings on the original fruiting tree was only partially successful. Four grafts were made in 1951. One of the grafted scions flowered in 1953 and again in 1954, but the other three scions have not yet bloomed.

Scions from the fruiting mother tree were grafted on the apomictic seed-

lings in 1951. The two surviving grafts flowered sparsely in 1953 at the age of three years, but did not flower in 1954. The fact that a scion from a young apomictic seedling grafted on the mature mother tree and the scions from the fruiting tree grafted on the apomictic seedlings produced flowers in the third year, as compared with six years for the seedlings, does suggest the presence of a flowering stimulating substance in the fruiting tree.

More critical evidence was obtained by budding genetically uniform dwarfing rootstocks with buds from both the fruiting hybrid 33340 and its apomictic seedlings. The dwarfing stock used was Ottawa 524 budded on *Malus sikkimensis*, an apomictic species which has been found to be semi-dwarfing when used as a rootstock. In 1951 buds from the hybrid 33340 mother tree and from its apomictic seedlings were budded on uniform rootstocks of Ottawa 524/*M. sikkimensis*.

The resulting trees were grown in the nursery for a year and then transplanted to a test plot. They were spaced six feet apart in a single row, alternating the five "old bud" with the five "young bud" trees. In 1953 one of the "old bud" trees produced flowers and fruits, but no flowers were produced by any of the other trees. In 1954 all of the trees from the "old buds" produced flowers and fruits, while no flowers were produced on any of the trees propagated from buds of the young seedlings. The data regarding flowering, fruiting, and tree size are shown in TABLE 1.

TABLE 1

Performance of trees from buds from an old fruiting tree (O), and from buds of a young apomictic seedling (Y) from the old fruiting tree. Budded in 1951 on Ottawa 524/*Malus sikkimensis*.

Tree Number	Source of Bud	Flower Clusters 1953	Flower Clusters 1954	Fruit 1954	Trunk Caliper cm. June 1954
1.	O	0	15	43	2.2
2.	Y	0	0	0	2.3
3.	O	21	34	103	1.9
4.	Y	0	0	0	2.2
5.	O	0	24	75	2.2
6.	Y	0	0	0	2.3
7.	O	0	42	104	2.2
8.	Y	0	0	0	2.3
9.	O	0	14	54	2.1
10.	Y	0	0	0	2.0
Ave.	O	..	26	76	2.1
	Y	..	0	0	2.2

There is no evidence that the initiation of flowering in the "old bud" trees was caused by the suppression of vegetative growth. Tree number 3 from an "old bud" was smaller than the adjacent "young bud" trees (num-

bers 2 and 4), presumably because it had borne a relatively heavy crop of fruit for such a small tree in the previous year. The four other "old bud" trees, which did not fruit in 1953, were no smaller than the adjacent "young bud" trees. All trees of both lots were identical in morphological characters.

The abundant fruiting of the "old bud" trees in the third year of growth may be due in part to the dwarfing rootstocks, yet the "young bud" trees on the same clonal rootstocks produced no flowers or fruits at the same age. Scions from the fruiting mother tree grafted on 33340 seedlings did produce some flowers the third year, whereas the original hybrid and several of its apomictic seedling progeny did not flower until the sixth year. Although the number of trees tested is small, the consistent results do suggest the transmission of some substance which promotes flowering in the buds or scions from the fruiting tree.

If there is transmission of a flowering hormone or "florigen" through the buds from fruiting trees, one might expect the "florigen" to be transmitted through the apomictic seeds from the mother tree. However, the transmission by vegetative propagation, but not by seed, is not inconsistent with the behavior of the viruses which are transmitted by grafting but not by seed.

The induction of flowering and fruiting can be stimulated in many ways, — by pruning or confining the root system, by grafting onto dwarfing stocks, by ringing or inverting the bark on the trunk of the tree, by knotting the stem, by training the branches in a horizontal position, and in some plants by vernalization or by changing the photoperiod. Only in a few cases has the artificial addition of auxin proved effective in promoting flowering. It is also possible that anti-auxin may play a role in flower induction and that vegetative growth and flowering are controlled by a balance between auxin and anti-auxin, but there is as yet little evidence to support this theory (1).

It seems improbable that all of the various flower-inducing techniques act in the same way. For example, the inversion of a ring of bark on the trunk of a young apple tree undoubtedly inhibits the flow of nutrients to the root system. But the inversion of a ring of bark on one of many branches of a large apple tree also checks vegetative growth and promotes fruiting of the branch involved, but has little or no effect on the rest of the tree. The checking of phloem transport by various means does affect the nutritional balance of the tree, but this is probably only one of a number of factors in promoting flowering.

The apparent transmission of a flowering stimulus by buds from fruiting trees may not be related to the production of flowers and fruits by the tree from which the buds are taken. Differences in tree vigor, size of the leaf associated with the bud, and differences in nutritional balance may be causal factors in promoting earlier fruiting. In order to test some of these possibilities buds from vigorous one-year-old McIntosh whips and buds from mature bearing McIntosh trees were budded on clonal rootstocks in 1951. Eight of each type were planted in a test plot at the Arnold Arboretum's Case Estate in Weston, but none has yet produced flowers. Since

the young whips came from buds from a fruiting tree their buds might be expected to transmit the "flowering hormone," even though the whips would not reach the fruiting age for several years.

We have also selected buds in August from a branch which had a section of bark inverted in June, and at the same time taken buds from a normal branch of the same tree and put these buds on clonal rootstocks. The branch with the bark inversion should flower earlier than the normal branches, and we might expect buds from the bark inversion branch to produce earlier fruiting trees than those from the normal branch, even though neither branch had ever borne flowers or fruits. These and other experiments in progress should provide more information on the nature of early induction of flowering.

SUMMARY

Buds from a fruiting apomictic ornamental apple tree and buds from its young seedlings were budded on uniform clonal dwarfing stocks in 1951. Of the five trees from the "old" buds, one flowered in 1953 and all flowered in 1954. None of the five trees from the "young" buds have yet produced any flowers. The earlier flowering of the trees from the "old" buds cannot be attributed to the suppression of vegetative growth. The evidence, although not conclusive, supports the assumption that a flower-stimulating substance was transmitted by the buds from the fruiting tree, but not by the apomictic seeds of the fruiting tree.

THE ARNOLD ARBORETUM AND
THE CABOT FOUNDATION

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RHODODENDRON MACROPHYLLUM D. DON EX G. DON

LEONARD F. FRISBIE

THERE IS BUT ONE SPECIES of *Rhododendron* with persistent or evergreen leaves that is native to the west coast of North America. A measure of confusion arising from a number of causes has prevented unanimous agreement as to the correct name of this species. In an effort to clarify matters The Tacoma (Wash.) Rhododendron Society, Inc., carried out a research project bearing on this problem. Results of this research were published by the Society in *Rhododendrons* 4 (9): 2-4. 1954. The present note is an attempt to bring this study to the attention of a wider public.

A complete synonymy of the species is to be found in "Bibliography of Cultivated Trees and Shrubs," by Alfred Rehder, p. 505, published by the Arnold Arboretum of Harvard University, 1949. With an understanding in mind that the International Code of Nomenclature assigns validity to the name used in the first published description without exception, it seems a very simple matter to observe that *Rhododendron macrophyllum* D. Don (1834) has precedence over *Rhododendron californicum* Hooker (1855). In fact it is a simple matter if one looks no further than Rehder's synonymy. The later epithet is in error, but circumstances in England surrounding the two published descriptions prove to be interesting indications of the reasons why the mistake was made.

David Don wrote the first description, using herbarium material. His younger brother, G. Don, published it in his "General System of Gardening and Botany" 3: 843. 1834. The description follows:

"*R. macrophyllum* (D. Don, mss. in herb. Lamb.) leaves lanceolate, acute, glabrous on both surfaces as well as peduncles, rounded at base; ovary bristly. Native of N. W. coast of America, where it was collected by Menzies. Petioles an inch long. Flowers copious, smaller than those of *R. maximum*, white. Calycine lobes short, rounded. Filaments glabrous. Long-leaved rhododendron. Shrub."

As will be noted, Don's description is rather incomplete and sketchy, and he considered the flowers to be white. Menzies makes no mention in his "Journal of Vancouver's Voyage" of having seen a white-flowered *Rhododendron*, and live material which he brought back to England proved to be pink-flowered. The designated color of the flowers in the description should have caused no confusion, but evidently it did. Dr. J. MacQueen Cowan of Scotland, who does the revision of *Rhododendron* classification for the Royal Horticultural Society, London, states that the color of the flowers of a *Rhododendron* species has no bearing on the validity of a first published description.

Don was evidently mistaken in stating that the filaments were glabrous. Field observations made in 1954 revealed that the filaments were pubescent

on the lower third in both the white-flowered and the pink-flowered forms.

Sir William Jackson Hooker did most of the work of describing and naming the plants which Menzies brought back from the northwest coast of North America, and his relation to the collection was semi-official. His description of the rhododendron was much more detailed than Don's. He worked from live material growing at Kew. Hooker published his description in the "Botanical Magazine," which has always had a place of great influence in British horticulture, and it was accompanied by a color drawing. These factors combined to give a very important place to Hooker's description when it was published in *Botanical Magazine* 81: *pl. 4863*. 1855. Hooker's description follows:

"*R. californicum*. Apparently a small or moderately sized shrub, with the habit of small plants of *Rhododendron maximum*, or still more of *Rhododendron catawbiense*, having stout branches, of which the younger ones are green and subherbaceous. Leaves on short petioles, three to four inches long, elliptical, obovate, acute, often almost mucronate at the point, tapering at the base, except in the upper leaves, glabrous and naked on both sides, paler colored on the under side. Beneath the flowers the leaves are generally more crowded, so as to form a sort of involucre to the large umbellate head. Calyx small, five lobed; the lobes form a broad base, almost subulate, slightly hairy. Corolla in bud rich carmine, when fully expanded broad campanulate; tube short suddenly spreading into five, broad, oval, crisped lobes; the ground color is then pale pink, deeper toward the apex of the lobes, and streaked with darker rose; thickened and downy below. Anthers deep pink. Ovary elliptical, with five longitudinal furrows, clothed with long, appressed silky hairs, five celled. Style rather larger than the stamens, glabrous. Stigma with five very minute points."

Hooker ignored Don's earlier description and his epithet was used in "Species of Rhododendron," published by the former British Rhododendron Association, and it has also appeared in successive editions of the "Rhododendron Handbook," now published by the Royal Horticultural Society. Rhododendron workers generally, including those of America, have followed these publications in the use of Hooker's epithet. The editor of Menzies' "Journal of Vancouver's Voyage," Dr. C. F. Newcombe, used *Rhododendron californicum*, marginal note, p. 20, the Preface XVIII, and also in the Appendix. The Washington state law designating this species as the State Flower makes the same error.

For some time, however, nearly all American scientists and botanists, and all herbaria, have correctly used *Rhododendron macrophyllum*. This is due in part to the influence of the published works of the late Alfred Rehder of the Arnold Arboretum.

All of the facts as stated above were presented to Dr. J. MacQueen Cowan and an appeal was made to him for a decision as to the correct epithet. He is positive that Don's *Rhododendron macrophyllum* has valid precedence, and that the use of *Rhododendron californicum* is in error. The Editors of the Royal Horticultural Society's publications in London have agreed to accept Don's epithet for use in future publications.

In the London publication, "Species of Rhododendron," p. 583, the statement is made: "*R. macrophyllum* is generally regarded as a form of this species with white and smaller flowers." Don stated in his description that the flowers were smaller than those of *R. maximum*. It is a mistake to infer that there is a difference in the size of the flowers of the two color forms. This same publication states: "HABITAT: California. On mountains at 1500 ft. altitude." This is an incomplete statement of the distribution of the species. The population in either Washington or Oregon is heavier than that of California. The species is known from southern British Columbia to Santa Cruz County, California. Populations in the coastal areas are exceedingly numerous.

While searching for exceptional forms of *Rhododendron occidentale* in Curry County, Oregon, in May 1954, field workers of the Tacoma (Wash.) Rhododendron Society, Inc., came upon a colony of seven plants of the extremely rare white-flowered form of this species (*R. macrophyllum*). The flowers were photographed and herbarium and propagating material was collected. An eighth member of the colony had been dislodged and left exposed to die by a logging bulldozer. Wood from the trunk of this plant was taken for an annular ring count. The diameter of the trunk was 3", and the age was 30 years. Details of this form are given below:

Rhododendron macrophyllum D. Don ex G. Don, f. *album* Rehder in
Jour. Arnold Arb. 28: 254. 1947.

HABIT: tall, growing to 30 ft., open, tree-like shrub sparsely branched.

LEAVES: elliptic to 18 cm. long, 7.5 cm. wide, cuneate at base, acute or mucronate at apex, glabrous on both surfaces, color lighter below.

INFLORESCENCE: 15 to 25 flowers, rachis ca. 1.5 cm. long.

COROLLA: pure white with dots on upper lobe, Sap Green HCC 62/1, clear color with no brown area as in type, 5 lobed, 5-6.5 cm. across, pedicel ca. 3.5 cm. long.

STAMENS: 10, 2-2.5 cm. long, pubescent below.

PISTIL: 3.75 cm. long, glabrous, ovary densely tomentose.

LOCALITY: northeast of Sixes, Curry County, Oregon, USA, on an abandoned logging road 600 ft. up the southwest slope of Sugarloaf Mountain.

COLLECTOR: Leonard F. Frisbie (Tacoma 1003), May 28, 1954.

NOTE: This specimen comparable with the typical species growing in the same locality except in color of flowers.

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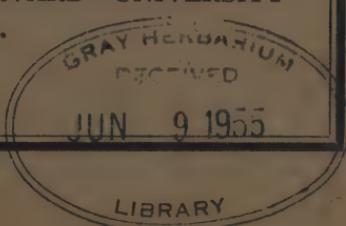


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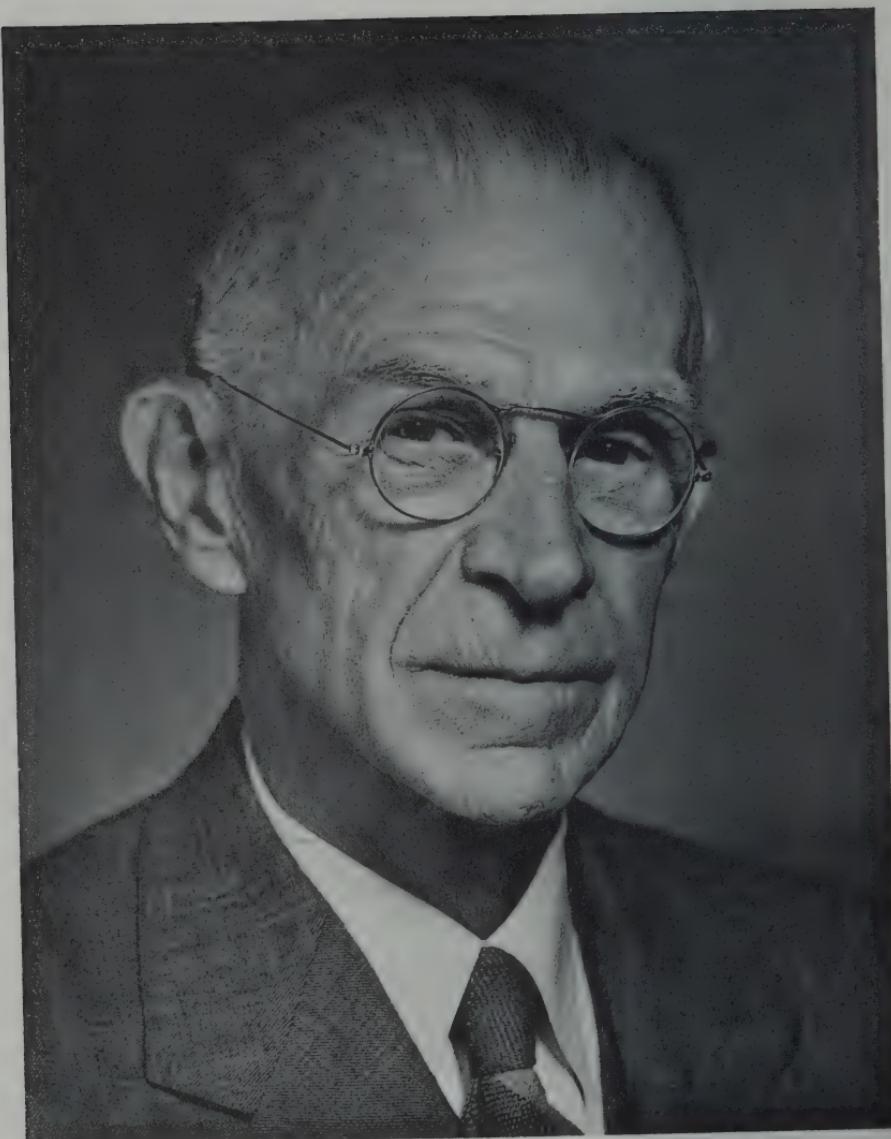
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CONTENTS OF NOS. 2 AND 3

DEDICATION [IRVING WIDMER BAILEY]. With portrait	i
THE COMPARATIVE MORPHOLOGY AND RELATIONSHIPS OF THE MAGNOLIACEAE — IV. WOOD AND NODAL ANATOMY. With three plates. By James E. Canright	119
THE TAXONOMIC USE OF SPECIALIZATION OF VESSELS IN THE METAXYLEM OF GRAMINEAE, CYPERACEAE, JUNCACEAE, AND RESTIONACEAE. With one plate. By Vernon I. Cheadle	141
THE POLLEN MORPHOLOGY OF SEVERAL GENERA EXCLUDED FROM THE FAMILY ICACINACEAE. With one plate. By A. Orville Dahl	159
THE SEED AND GINKGO. By Arthur J. Eames	165
SOME FACTORS IN POLLEN GERMINATION: CALCIUM SALTS, DEXTROSE, DRYING. By Anna F. Faull	171
COMPARATIVE MORPHOLOGY OF THE FOLIAR SCLEREIDS IN BORONELLA BAILL. With five plates. By Adriance S. Foster	189
A TAXONOMIC REVISION OF PODOCARPUS. IX. THE SOUTH PACIFIC SPECIES OF SECTION EUPODOCARPUS, SUBSECTION F. With one plate. By Netta E. Gray	199
THE VEGETATION OF BEATA AND ALTA VELA ISLANDS, HISPANIOLA. With five plates. By Richard A. Howard	209
ON THE PRIMARY VASCULAR SYSTEM AND THE NODAL ANATOMY OF EPHEDRA. With three plates. By Margery P. F. Marsden and Taylor A. Steeves	241
THE OCCURRENCE OF EUPTELEA IN THE CENOZOIC OF WESTERN NORTH AMERICA. With three plates. By Richard A. Scott and Elso S. Barghoorn	259
STALK DIAMETER AS A FACTOR IN FRUIT SIZE. By Edmund W. Sinnot	267
PHANEROGAM GENERA WITH DISTRIBUTIONS TERMINATING IN FIJI. By A. C. Smith	273
MITOCHONDRIA AND PRECIPITATES OF A-TYPE VACUOLES IN PLANT CELLS. With three plates. By Helen P. Sorokin	293
ON THE DIFFERENTIATION OF XYLEM. With six plates. By Ralph H. Wetmore and Sergei Sorokin	305

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IRVING WIDMER BAILEY

DEDICATION

On the occasion of the retirement of PROFESSOR IRVING WIDMER BAILEY after twenty-two years on the staff of the Arnold Arboretum and forty-seven years of service to Harvard University, we, his associates on the editorial board of the Journal of the Arnold Arboretum, dedicate this issue to him.

The authors of the articles in this special number of the Journal represent only a few of the students and associates of Professor Bailey who would pay tribute to him at this time. We honor him with this issue in recognition of his contributions, his high standards of research, his integrity in science and personal life, and his guidance of and inspiration to students in the field of botany.

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THE COMPARATIVE MORPHOLOGY AND RELATIONSHIPS OF THE MAGNOLIACEAE—IV. WOOD AND NODAL ANATOMY

JAMES E. CANRIGHT

With three plates

INTRODUCTION

THE MORPHOLOGICAL AND ANATOMICAL CHARACTERISTICS of the magnolia family have attracted the interest of many investigators over a long period of time. This interest stemmed not only from the supposed antiquity of the Magnoliaceae, but also from the group's phylogenetic importance in many systems of classification.

Some of the earliest work on the anatomy of the Magnoliaceae was that of Matsuda (34), Gröppeler (25), and Parmentier (42). Undoubtedly the most detailed description of any magnoliaceous wood was by Moll and Janssonius (37) on seven Javanese species. Solereder's (51) anatomical descriptions were based almost entirely on twig material removed from herbarium sheets, therefore the recent publication of Metcalfe and Chalk (36) is of considerably more value, since mature woods of five of the ten genera of Magnoliaceae (*sensu stricto*) were examined. McLaughlin (35) has made one of the most important contributions, due to the fact that his wood descriptions were based on a study of 40 species (of some 200 now recognized for this family). Other papers bearing on this topic by Lemesle (31) and Ozenda (41) have recently appeared.

Despite all of the above-mentioned reports, the true phylogenetic value of the woods of the Magnoliaceae, in the light of modern knowledge, still remains to be fully evaluated.

In 1940, following 30 years of intensive anatomical research on such basic problems as the ontogenetic and phylogenetic significance of the cambium and its derivatives, nodal anatomy, cell wall structure, and many related subjects, Professor Irving W. Bailey launched a series of cooperative investigations on both reproductive and vegetative organs of dicot families belonging to the order Ranales (*sensu Engler*). These extensive surveys were made possible by Prof. Bailey's long and active interest in building up the Harvard Slide Collections; these included not only a large

and diversified assemblage of wood, pollen, and leaves, but also some floral organs and seedlings. In this connection, it goes without saying that the living collections and herbarium specimens of the Arnold Arboretum were an invaluable source of much of the plant material.

As a result of the Bailey-stimulated interest in the Ranales, during the past 13 years a number of comprehensive papers by Bailey, his colleagues and students have appeared. These papers delineate the morphology, trends of specialization, and natural relationships of the following woody ranalean families: Degeneriaceae (8, 54); Winteraceae (4); Himantadraceae (7); Trochodendraceae and Tetracentraceae (5, 49); Eupteleaceae (39); Illiciaceae and Schisandraceae (6, 50); Cercidiphyllaceae (55); Magnoliaceae (11, 12); Austrobaileyaceae (9); and Monimiaceae (38).

Indeed, an examination of recent taxonomic works, e.g., Gunderson (26), Stebbins (52), pp. 8-9, and Lawrence (29), clearly indicates the profound influence the findings of the "Bailey school" have had on present-day concepts of the woody Ranales.

The present paper is respectfully dedicated to Prof. I. W. Bailey upon the occasion of his retirement from active teaching, since it was he who first fostered my interest in ranalean plants, and who has encouraged and helped me in innumerable ways.

MATERIALS AND METHODS

As interpreted by Dandy (17), the Magnoliaceae include 10 genera and perhaps as many as 210 valid species. *Magnolia* is the largest genus, comprised of about 80 temperate and tropical species, of which 24 are American and the rest Asiatic in distribution. *Talauma*, containing about 42 species, also is characterized by a split distribution; however, only nine species occur in tropical America, with the remainder being scattered throughout Malaysia. *Liriodendron* has two temperate species — one in eastern North America and one in central China. All other genera normally grow within an area extending from the Himalayas to China and Japan, southward through Burma, Malaya, Indo-China, Siam, Indonesia, and the Philippines, to northern New Guinea. *Michelia* includes about 50 species; *Manglietia*, 25; *Elmerrillia*, 7; *Aromadendron*, 3; *Kmeria*, 2; *Pachylarnax*, 2; and *Alcimandra* is monotypic.

In the survey of mature woods of this family, transverse, radial, and tangential sections were examined from 61 species in seven genera. In addition, transverse and longitudinal sections were made from twigs (4-6 mm. in diameter) from herbarium specimens of the rare genera *Alcimandra* and *Kmeria*. Thus, only *Pachylarnax* was not represented. This investigation included all slides and wood samples of the Magnoliaceae in the Harvard wood collection, as well as the collections of the Yale School of Forestry.¹

In order to check the ranges of variability of the wood characters in each genus, 5" × 8" punch cards (Y-9 Unisort Analysis Cards from the Chas.

¹ The writer is indebted to the curators of these collections for the loan of material.

R. Hadley Co., Los Angeles) were utilized for each species. Around the margins of these cards are 94 numbered perforations which were keyed to the most important diagnostic features of woods as listed by Record and Chattaway (45). In examining each wood slide microscopically, whenever a certain feature was present, the numbered hole on the card referring to this feature was notched. After the entire wood survey was completed, this notch allows the card to drop out of the stack whenever a spindle is inserted in that hole, thereby indicating the presence of that particular feature in that species. The punch card method also proved of value in the revelation of several wood specimens which had apparently been wrongly identified in the past. In the event that herbarium vouchers are not in existence for questionably-identified wood slides, this punch card method offers one of the best means of identification.

The number of wood macerations made was insufficient to allow reliable utilization of vessel element length as a feature of phylogenetic importance. The wood ray types proposed by Kribs (27) and the wood parenchyma classification of Bailey and Howard (3) are followed here; in all other cases the terminology follows that recommended by the Committee on Nomenclature of the International Association of Wood Anatomists (15).

Transverse nodal sections of 25 species were cut serially, commencing from below the node and passing up through the petiole, in order to ascertain the vascular pattern. The majority of these twigs were sectioned unembedded at 24μ on a sliding microtome. However, due to their extreme hardness, twigs of about ten species (mainly talaumas and manglietias) had to be softened in hydrofluoric acid and embedded in celloidin before sectioning was possible.

The serial order of the nodal and petiolar sections was maintained by placing the sections in a linear sequence on a glycerine-covered slide immediately after each section was cut. The slide was then covered by a piece of fine mesh stainless steel wire cloth, which was held on by means of a wooden clip. This wire cloth did not appreciably interfere with later dehydration or staining procedures. The sections were then stained in safranin or else mounted unstained in diaphane.

ANATOMICAL DESCRIPTIONS OF THE GENERA

Of the 40 species examined by McLaughlin (35), 35 belonged to the genera *Magnolia*, *Michelia*, and *Talauma*. Since McLaughlin's descriptions of these three genera are substantially correct, the present treatment will refer to these genera only whenever our observations seem to be at variance, or else to supplement portions of the previous descriptions.

Alcimandra Dandy

Diffuse porous; growth rings indistinct; pores angular in cross section, thin-walled, small (ca. 47μ in diameter), solitary to radial chains of 2-3, numerous, *Fig. 5*; perforation plate scalariform, 8-15-barred; intervascular pitting scalariform with traces of opposite pitting in older wood; wood

parenchyma apotracheal, in tangential bands 2–4 cells wide; fiber tracheids, pits with crossing slit-like apertures whose length equals the diameter of the pit border; wood rays, Heterogenous Type I — tall uniserials composed mainly of upright cells, and tall (up to 100 cells) and narrow (2–3 cells) multiseriates; oil cells absent. Description based on *Alcimandra cathcartii* (Hk. f. & Thoms.) Dandy collected by J. D. Hooker without number from Sikkim (H-27724).

Alcimandra cathcartii (Hk. f. & Thoms.) Dandy was originally referred to the genus *Michelia* on account of the stipitate gynoecium and character of the fruit, but Dandy (17) separated it out because it was the only *Michelia* species characterized by terminal flowers. The wood of this plant is essentially like that of *Michelia* with the following exceptions: the pores are smaller, there are more bars in the perforation plate; the rays are taller, and ethereal oil cells are lacking. However, these differences, for the most part, may be ascribed to the lack of maturity of the *Alcimandra* material examined, i.e., the differences may be ontogenetic not phylogenetic ones.

Aromadendron Blume

Diffuse porous; growth rings faintly visible (due to slight thickening of radial walls in late wood elements); pores essentially solitary, oval in outline, very large (up to 240μ in tangential diameter), Fig. 1; perforation plate scalariform, 6–10-barred; intervacular pitting scalariform, with some reticulations, Fig. 22; tyloses not uncommon; spiral thickenings present; wood parenchyma terminal or initial in rows of 4–5 cells; fiber tracheids, with crossed apertures slightly extended; Heterogeneous Type IIA rays; multiseriates 2–3 cells wide and 15–40 cells high, with oil cells of fairly common occurrence on their margins; oil cells may also infrequently occur within body of uniserial rays composed of upright cells, Fig. 16.

Above description based on mature wood of *A. elegans* Bl. (H-22787) and twig material (H-27725).

McLaughlin's (35) statement that the wood of this genus contains no marked characteristics separating it from that of *Talauma* is not substantiated by the present study. The pores in *Aromadendron* are the largest in the entire family, and are almost twice the size of the pores in any of the investigated Asiatic *Talauma* spp. Differences are also apparent in the wood parenchyma distribution and fiber tracheid characteristics of the two genera. Finally, a cursory comparison of floral and fruit types is sufficient in this case to refute McLaughlin's unigenetic views.

Elmerrillia Dandy

Diffuse porous; growth rings usually indistinct; pores solitary, Fig. 2 (but with some tendency towards formation of radial chains), oval in outline, medium to large (135 – 220μ); perforation plate scalariform, 4–10-barred; intervacular pitting scalariform; parenchyma terminal or initial, in rows of 3–4 cells; fiber tracheids with pit apertures included or slightly

extended; rays, Heterogeneous IIA and IIB (complete elimination of uniserials in *E. mollis*); multiseriate rays mainly biserrate and 15–40 cells high; oil cells common in margins of rays, *Figs. 13, 15*.

Description based on *E. mollis* Dandy (H-25694), *E. ovalis* (Miq.) Dandy (H-25695 and Y-19509), and *E. papuana* (Schltr.) Dandy (H-27728).

The wood of this genus falls within the range of variability of the woods of *Michelia*, which *Elmerrillia* also most closely resembles in exomorphic characters.

Kmeria Dandy

Diffuse porous; pores solitary to multiples, numerous, *Fig. 6*; vessel diameter small (52μ); perforation plate scalariform, 8–12-barred; intervascular pitting scalariform; parenchyma thick-walled, apparently terminal, in rows of 2–3 cells; fiber tracheids; rays heterogeneous (exact size not determinable); oil cells absent.

Above description based on $1\frac{1}{2}$ yr. old twig of *K. duperreana* (Pierre) Dandy, 6 mm. in diameter (H-27730) from Indochina.

Although the wood of this genus is indistinguishable from that of many tropical *Magnolia* spp., Dandy's (17) transfer of *Magnolia duperreana* into a new genus based on its possession of unisexual flowers seems valid in this otherwise hermaphroditic family.

Liriodendron L.

The wood of this genus is sufficiently well known, therefore only a brief comparison of the anatomy of the American and Chinese species seems warranted. In general the two woods are quite similar, but the following differences are noted: in *L. chinense* the pores tend to be less numerous, more rounded, thicker-walled, and smaller in diameter (85μ) than those of *L. tulipifera* (120μ in diameter). The difference in thickness of walls of the fiber tracheids and the diameter of the pores in the late wood as compared to the early wood is much more pronounced in *L. chinense* than in the American species. The size of the early wood pores of the Chinese species is almost twice that of the late wood pores, whereas in the American species there is no appreciable difference in early and late wood pore size, *Fig. 7*. There are more and larger pits (border = 7μ) in the walls of the fiber tracheids of *L. chinense*, whereas the fiber tracheid pits in *L. tulipifera* average only 3.5μ and the apertures are commonly included. Tyloses are numerous in vessels of *L. tulipifera* and absent in *L. chinense*. The 2–3-seriate rays of the latter species tend to be fairly uniform in size, rarely ranging over 20 cells high. On the other hand, the rays of *L. tulipifera* tend to be slightly broader (3–4-seriate) and often reach heights of 25–35 cells, mixed in with many shorter rays, *Fig. 17*.

Material examined: *L. chinense* (Hemsl.) Sargent (Y-21461, H-27731); *L. tulipifera* L. (H-3759, H-24492, H-24675, and H-24674).

It is entirely possible that insufficient sampling makes these differences

in the wood of the two species more apparent than real. Nevertheless, the information should at least be taken into consideration by certain systematists who feel that the exomorphic characters of the Chinese species are insufficient bases for specific rank.

Magnolia L.

Some outstanding features of the wood of this familiar genus are: growth rings clearly apparent in the temperate species due to the prominent bands of terminal (or initial) parenchyma, but inconspicuous in many tropical species, e.g., *M. paenetalaura* from Hainan, *Fig. 4*. This species is also noteworthy in that it possesses the smallest pores (48μ) seen in mature woods of this family. The pore diameter of all other investigated species in this genus ranges from $65-120\mu$. With the exception of *M. poasana* (Pitt.) Dandy, which is characterized by solitary, sparsely-distributed pores (only $8-10/\text{sq. mm.}$), the pores of *Magnolia* spp. are numerous, crowded, and often in dense radial chains or clustered. Although the majority of magnoliaceous species have scalariform perforation plates (6-12-barred), simple perforations in oblique end walls occur in certain temperate species — *M. acuminata*, *M. campbelli* (*Fig. 10*), *M. cordata* (*Fig. 9*), *M. kobus* DC., *M. obovata*, *M. soulangeana* (*M. denudata* Desr. \times *M. liliiflora* Desr.), and *M. stellata* Max. Tyloses rare, but present in *M. cordata*, *M. pterocarpa*, and *M. tripetala*. Spiral thickenings prominent only in *M. grandiflora*, *M. hamori*, and *M. paenetalaura*. Intervascular pitting scalariform to transitional, with only *M. fraseri* having strictly opposite pitting. Parenchyma apparently terminal (3-8 rows) in temperate species, but the narrow-banded apotracheal type is not uncommon in some tropical species, e.g. *M. cubensis*; in most species the radial walls of the parenchyma strands are highly sculptured, *Fig. 18*. Pits on fiber tracheids may have either included or extended slit-like apertures. Rays Heterogeneous Type IIA and IIB, except in three temperate species which are characterized by more advanced Homogeneous Type II rays (*M. acuminata*, *M. kobus*, and *M. obovata*). Oil cells seen only in rays of *M. cubensis*, *M. hamori*, and *M. splendens* — all from the West Indies.

Wood examined from 22 species as follows: *M. acuminata* L. (H-17352, H-18963); *M. campbelli* Hk. f. & Thoms. (H-4395L); *M. cordata* Sarg. (H-8968); *M. cubensis* Urb. (Y-19283); *M. fraseri* Walt. (H-17353); *M. grandiflora* L. (H-8972, H-17355); *M. gustavii* King (H-27770); *M. hamori* Howard (*Hamor* without number); *M. javanica* Koord. & Val. (H-17356); *M. kobus* DC. (H-17359); *M. macrophylla* Michx. (H-8979); *M. obovata* Thunb. (H-8981, H-8974); *M. paenetalaura* Dandy (H-21111); *M. parviflora* Sieb. & Zucc. (H-27736); *M. poasana* (Pitt.) Dandy (Y-38423); *M. pterocarpa* Roxb. (H-17360); *M. soulangeana* HORT. (H-21018); *M. splendens* Urb. (H-1713); *M. stellata* Max. (H-21306); *M. tripetala* L. (H-8983, H-17362); *M. virginiana* L. (H-1712, H-8970).

Manglietia Blume

Growth rings indistinct; pores solitary to radial chains of 2-5; vessel diameter in mature wood generally 120-155 μ ; perforation plate scalariform, 5-12-barred; intervacular pitting scalariform to transitional, *Fig. 23*; parenchyma terminal or initial in rows 2-6 cells wide; fiber tracheids, pit apertures included or slightly extended; rays of Heterogeneous Type IIA, mainly 2-3-seriate and up to 40 cells high; oil cells absent.

A wood supposedly belonging to *M. fordiana*, *Fig. 24*, (det. by W. C. Cheng of the Fan Inst. of Biology) differs from the above generic description in several important characters; pores small (60 μ), numerous, crowded together in no definite pattern; scalariform perforation plate only 1-6-barred; growth rings distinct; Heterogeneous IIB rays.

Material examined: *M. caveana* Hk. f. & Thoms. (H-27743); *M. chevalieri* Dandy (H-27744); *M. conifera* Dandy (H-27746); *M. dandyi* Gagnep. (H-27747); *M. fordiana* Oliv. (H-27748, Y-31907); *M. glauca* Bl. (Y-30038); *M. hookeri* Cub. & W. Sm. (H-27750); *M. insignis* (Wall.) Bl. (Y-9580, H-27752).

McLaughlin's statement (35) that *Manglietia* may be only a subgenus of *Talauma* gains no support from this investigation. Indeed, if any fusion of genera were attempted, it would seem more logical to combine *Manglietia* with *Magnolia*. There is little difference in the wood anatomy of *Manglietia* and many temperate *Magnolia* spp.; in addition, the only clear-cut difference in floral characters lies in the number of ovules/carpel — (2 in *Magnolia*, and 4-14 in *Manglietia*).

Michelia L.

Minute anatomy as described in McLaughlin (35) with the following exceptions or addenda: pores solitary or in radial chains of 2-5, except *M. maudiae* and *M. lanuginosa* which have pores in clusters; pore diameter of largest elements in mature woods ranges from 70 μ in *M. maudiae* to 220 μ in *M. lanuginosa*; perforation plates always scalariform, 1-6-barred, *Fig. 8*; tyloses occur only in *M. baillonii*, *M. balansae*, and *M. oblonga*; spiral thickenings very common in 8 of 12 examined species (absent only in *M. figo*, *M. lanuginosa*, *M. montana*, and *M. oblonga*); distribution of wood parenchyma is more variable in this genus than in any other in this family; although terminal or initial bands (in 2-6 rows) are most common, *M. figo* has closely-spaced single rows of apotracheal parenchyma, and *M. champaca* has some scanty paratracheal, ranging to abaxial types in the late wood of *M. baillonii*, *Fig. 21*; fiber tracheids usually thick-walled and with pit apertures more or less extended; rays Heterogeneous Type IIA and IIB; uniseriates rare (to none in *M. tsoi* and *M. baillonii*), never over 10 cells high; multiseriates 2-3 cells wide, rarely over 25 cells high, and usually bearing oil cells among the upright marginal cells.

Material examined: *M. baillonii* (Pierre) F. & G. (Y-13251); *M. balansae* (A. DC.) Dandy (Y-12914); *M. champaca* L. (H-1016); *M.*

compressa (Max.) Sarg. (H-23170); *M. foveolata* (Merr.) Dandy (H-21081); *M. fuscata* Bl. (H-15777); *M. figo* (Lour.) Spreng (Y-22012); *M. lanuginosa* Wall. (Y-30043); *M. maudiae* Dunn (H-21085); *M. montana* Bl. (Y-19506, H-17365); *M. oblonga* Wall. (Y-9570); *M. tsoi* Dandy (H-21079).

The wood from China which was identified as *M. figo* (Y-22012, Fan Memorial Inst. #0544) has a number of anatomical features, including alternate intervacular pitting, which are inconsistent with other woods in this family, let alone the genus *Michelia*. Although *M. fuscata* Bl. is putatively a synonym for *M. figo* (Lour.) Spreng., due to the many anomalous features found in the wood specimen supposedly belonging to the latter species, the present author was unable to verify the synonymy. Unfortunately, no herbarium voucher was deposited with this Chinese wood specimen; thus a recheck on the original determination was impossible in this case.

Talauma Juss.

Growth rings absent; pores solitary to some radial chains of 2-3, rounded or oval; pore diameter varies from 65μ (*T. hodgsoni*) to 205μ (*T. gloriensis*); perforation plate scalariform, 8-20-barred; intervacular pitting scalariform with some transitional; tyloses present in 8 of the 12 examined species, and some sclerotic tyloses were found in *T. angatensis*, *T. gigantifolia*, *T. sambuensis*, and *T. villariana*; spiral thickenings present only in *T. mexicana*; parenchyma apotracheal narrow-banded (1-4 cells), bands often closely-spaced, being only 170μ apart in *T. villariana*, Fig. 25; fiber tracheids, thick-walled, pit borders much reduced and apertures greatly extended; rays of Heterogeneous Type I and IIA, uniseriate rays composed of upright cells, multiseriates up to 4 cells wide and 40 high; oil cells occur in rays of seven species.

Above description based on examination of: *T. angatensis* (Blanco) F. Vill. (Y-19995, H-27761); *T. candollei* Bl. (H-15783); *T. dodecapetala* (Lam.) Urb. (H-27763); *T. gigantifolia* Miq. (H-3761J); *T. gloriensis* Pitt. (Y-38448); *T. hodgsoni* Hk. f. & Thoms. (H-15787); *T. mexicana* Don. (H-27765); *T. minor* Urb. (Y-19313); *T. mutabilis* Bl. (H-17377); *T. rumphii* Bl. (Y-19510); *T. sambuensis* Pitt. (H-1711, from type tree); *T. villariana* Rolfe (Y-17148).

DISCUSSION OF WOOD ANATOMY

Just as in the case of the stamens (11) and pollen (12) of this family, there is a considerable degree of generic overlap in the characters of phylogenetic importance. [For a concise summation of the evolutionary trends known for woods, see Tippo (56)]. In other words, all the primitive characters are not confined to any one genus, nor are all the advanced characters. Nevertheless, on the basis of the present wood survey, there are many indications that the woods of the temperate species of *Magnolia* and *Lirio-*

dendron are the most specialized, with most tropical species of *Talauma* exhibiting the largest assemblage of primitive characters. As previously noted in the generic descriptions of the woods, certain temperate species of *Magnolia* have the following advanced² characters: numerous crowded pores, porous perforation plates, Homogeneous Type II rays, and in one case, strictly opposite intervacular pitting. *Liriodendron* also shows this last-named feature. On the other hand, certain species of *Talauma* are characterized by the following primitive features: solitary sparsely-distributed pores, up to 20-barred perforation plates, elongate vessel elements, apotracheal narrow-banded parenchyma, and Heterogeneous I or IIA rays.

It is of interest to note a rough correlation between the stage of evolution represented by the woods of many temperate magnolias with that determined independently by Dandy (18) based solely on exomorphic characters. The most advanced *Magnolia* subgenus (Pleurochasma) contains three sections (*Yulania*, *Buergeria*, and *Tulipastrum*) which include such anatomically-advanced species as *M. acuminata*, *M. cordata*, *M. kobus*, *M. campbelli*, and *M. stellata*. By way of comparison, *Magnolia paenetaluma* from tropical Hainan exhibits a number of primitive features, such as small solitary pores, long vessel elements with many-barred (up to 16) perforation plates, and extremely tall (over 100 cells) heterogeneous rays. Dandy (*loc. cit.*) has placed this species in the first section (*Gwillimia*) of the more primitive subgenus *Magnolia*; in so doing he remarked that the members of this section resemble those of the genus *Talauma* in so many ways that the generic position of some of the species is uncertain in the absence of fruiting material.

However, it should be emphasized that this apparent correlation between external and internal characters is not always present, since rates of floral and vegetative evolution do not necessarily progress at the same pace. In this connection, Bailey (2) has recently warned of the dangers inherent in jumping to conclusions concerning plant phylogeny and classification based on inadequate anatomical data from a single organ or tissue. Unfortunately, in working on the woods of the Magnoliales, McLaughlin (35) fell into this pitfall; although his observations are basically sound, he assumed too much from the examination of wood specimens alone. For example, he recommended that *Aromadendron* and *Manglietia* be reduced to subgenera of *Talauma*, and that *Elmerrillia* and *Alcimandra* be similarly reduced to *Michelia*. These proposed major shifts in the classification of this family were based solely on the evidence gleaned from not more than five wood specimens from the four above-mentioned "doubtful" genera. Furthermore, McLaughlin reduced 10 species to synonymy without benefit of study of herbarium specimens. In view of situations of this type, it is little wonder that certain taxonomists — specialists on one group or another — have little respect for anatomical research; in fact, may even literally lock their doors (and herbarium cases) whenever an anatomist

² Applied here in the sense that these characters are advanced in relation to the wood characters in the family as a whole. No magnoliaceous woods are highly evolved when compared to those of all angiosperm families.

approaches and requests their cooperation and advice. As Bailey (1) has pointed out, due to the widely-occurring cases of parallel evolution in the woods of dicotyledons, evidence from the vascular tissues, by itself, proves to be more significant in negations than in affirmative conclusions.

Lemesle (30, 31) claimed discovery of a new type of tracheary element in the xylem of the ranalean genera *Schisandra*, *Kadsura*, and *Illicium*. This type of element was distinguished from the more common fiber tracheids in other ranalean genera by the fact that these "cycad-like tracheids" were characterized by bordered pits whose crossed apertures were usually smaller than the borders. He further postulated that this type of element was much more archaic than the fiber tracheids of the Magnoliaceae, since the latter elements had circular bordered pits whose crossed apertures equaled or exceeded their borders. Finally, upon the unsubstantiated assumption that the characters of the fibers are more constant and unchangeable than those of the vessels, Lemesle (30) proposed a linear phylogenetic sequence, deriving the Magnoliaceae from the Bennettitales by way of the "Proangiosperms", "Homoxyloleae" [Van Tieghem's (57) unnatural grouping of vesselless angiosperms], Schisandraceae, and Illiciaceae.

Although the present author has recorded for the fiber tracheids of the Magnoliaceae whether the pit apertures are generally included or extended, no phylogenetic import is attached to these features. Indeed, it seems probable that the size of the obliquely oriented slit-like apertures depends to a certain extent on the amount of shrinkage of the wood samples caused by drying prior to sectioning. The oblique or helical orientation of the microfibrils of cellulose in the secondary walls of tracheary elements, as observed by Bailey and Vestal (10) and Maby (32), lends considerable support to this conclusion.

The distribution of the wood parenchyma in the Magnoliaceae is commonly referred to as terminal (36, 46). This type, according to Kribs (28), represents a specialization due to reduction, since there is no correlation with any one vessel type. Furthermore, this type of parenchyma distribution occurs indiscriminately throughout many dicotyledonous families.

Coster (16) mentions his belief that terminal parenchyma formation has a direct physiological relationship to the annual drop of leaves in deciduous forms. Obviously, however, this explanation cannot be valid for non-deciduous tropical members of the Magnoliaceae characterized by terminal parenchyma. Chowdhury (13, 14) has made ontogenetic investigations of diffuse porous tropical woods putatively bearing terminal parenchyma; he has been able to show in many cases (e.g., *Terminalia tomentosa*, *Dalbergia sissoo*, *Swietenia macrophylla*, *Salix matsudana*, etc.) that the wood parenchyma bands actually form in the beginning of each year's growth ring, thus should be referred to as initial, not terminal. In the light of this evidence, the present author preferred to use the phraseology "terminal or initial" in describing the wood parenchyma of most magnoliaceous species, at least until such time as this feature can be thoroughly investigated from an ontogenetic standpoint. The fact remains, however, that both terminal

and initial patterns of parenchyma distribution are undoubtedly specialized types, conceivably having been formed by means of a reduction series from either paratracheal or apotracheal types. Therefore, the usual absence of terminal or initial parenchyma in the wood of examined species of *Talauma* indicates another primitive character for the wood of this genus.

The phylogenetic value of spiral thickenings on the secondary wall of vessels is still a controversial matter. Frost (22) and Stern (53) regard spiral thickenings as an advanced character, yet Metcalfe and Chalk (36) from an examination of over 3000 woods state that this feature is about twice as common in unspecialized as in specialized woods. Further, the latter authors' statistics reveal that spiral thickening is often linked with ring porosity, occurring in 44% of the ring porous woods, and only in 6½% of diffuse porous woods. Record (44) states that spiral thickenings are much less common in tropical woods than in temperate woods, which concurs with the above statistics of Metcalfe and Chalk. Petersen (43), after a comparison of woods belonging to the advanced Amentiferae and the primitive Ranales, found this feature equally divided between the two groups.

The data from the woods of the Magnoliaceae lend little support to either concept regarding the significance of spiral thickenings. This feature was present in vessels of only 14 species of 61 examined, and was more common in *Michelia* (in eight of 12 species) than in any other genus. Although wood of *Michelia* seems to be more specialized (viz., 1-6-barred perforation plates, occurrence of pore multiples, thick-walled fiber tracheids, and tendency toward paratracheal parenchyma) than other tropical magnoliaceous genera, the sampling is insufficient to warrant an interpretation of the phylogenetic value of spiral thickenings. In addition, the fact that Metcalfe and Chalk (*loc. cit.*) list this character for 101 widely separated families of dicotyledons, tends to further invalidate conclusions of evolutionary importance.

Similarly, the presence or absence of tyloses is only of diagnostic, and not phylogenetic, value. This feature was found in 18 species, being most common in *Talauma* (in eight of 12 examined species), where four species even exhibited sclerotic tyloses.

Oil cells are common features in the rays of most magnoliaceous species, being absent only in examined species of *Alcimandra*, *Kmeria*, *Liriodendron*, and *Manglietia*. However, since oil cells are also of common occurrence throughout all organs of most ranalean families, their presence in woods of the Magnoliaceae is of no special significance.

As previously noted by Bailey et al (7), the woods of the Degeneriaceae, Himantandraceae, and Magnoliaceae are of a basically similar type, differing markedly from that which occurs in other ranalean families, with the possible exception of the Annonaceae. The wood of Degeneriaceae is of a comparatively primitive type; that of the Magnoliaceae shows transitional stages from the *Degeneria* type up to comparatively advanced types with porous vessels and homogeneous rays; the wood of *Himantandra* most

closely compares with some of the more advanced members of the Magnoliaceae in its possession of both scalariform and porous vessels, plus intervacular pitting transitional between opposite and alternate. The regular occurrence of sclerotic pith diaphragms in all three families is also noteworthy.

PHLOEM

Esau et al (21) have recently discussed the manifold problems involved in attempting to establish reliable trends of specialization for phloem tissues. One of these problems concerns the collapse of leptom (soft-walled) tissue upon drying, which naturally makes observation of its details difficult, if not impossible.

When living secondary phloem is properly fixed, the alternate stratification of leptom and fibrous tissue is plainly evident in certain temperate magnoliaceous species, e.g., *Liriodendron tulipifera*, Fig. 3. Furthermore, the prominent sieve tube elements and companion cells are separated from the thick-walled phloem fibers by tangentially aligned uni- or biserrate rows of phloem parenchyma. A similar arrangement has been observed in phloem of *L. chinense*, *Manglietia* spp., and *Michelia champaca*. However, this precise arrangement of phloem tissues is less clear in other tropical species of the Magnoliaceae (perhaps due in part to poor preservation of phloem in the examined species), and seems to be absent entirely in *Alcimandra*. In the latter genus bands of phloem fibers extend radially, instead of tangentially, more or less flanking the sieve tube elements. Therefore, although the evidence is admittedly fragmentary, it is suggested that the occurrence of alternate tangential banding of leptom and fibrous tissues in the secondary phloem of dicotyledons may be a further trend of specialization.

Among the Magnoliaceae the conspicuous V-shaped flaring of the phloem rays (as viewed in cross section) is usually associated with the type of tangentially banded phloem mentioned above. It is significant that such V-shaped rays and alternate hard and soft bast layers have already been noted in the Degeneriaceae (8) and Himantandraceae (7).

MacDaniels (33) has described the sieve tube element of *Magnolia acuminata* and *Liriodendron tulipifera* as being characterized by 6–10 rounded sieve areas situated on an oblique end wall. This type of sieve tube element he termed Type II, i.e., slightly more specialized than Type I (very oblique end walls containing 10–20 sieve areas). Thus, for these two species the level of specialization for this phloem element roughly parallels that of the vessel elements. However, in view of the fact that the woods of these two species are among the most advanced in the family, it would seem desirable to withhold final judgment on this matter until well-preserved phloem of some of the more primitive tropical magnoliaceous species can be thoroughly investigated.

NODAL ANATOMY

The nodal anatomy of the Magnoliaceae is rendered quite complex due to the constant occurrence of sheathing stipules together with a large number of stipular traces. However, in the node of members of the tribe Magnolieae (of Dandy, 17) there is usually only one trace whose sole function is the vascularization of the stipular sheath;³ this trace is located on the opposite side of the caudine stele from the large median trace to the leaf, *Fig. 19*. In the case of *Liriodendron tulipifera* (tribe Liriodendreae) Ozenda (40) has demonstrated that each of the six lateral traces also sends small amounts of vascular tissue into the stipular sheath. Nevertheless, since the main vascular supply of these lateral traces passes almost horizontally around the stele and into the margins of the petiole, when serial sections are examined the median and lateral traces are readily distinguishable from the stipular trace.

In the base of the petiole of all examined species the traces split up in a variable fashion, and some of the bundles may become inverted. No matter how variable the pattern in the base of the petiole, the bundles ultimately form a ring as they near the base of the lamina. The occurrence of a few medullary and/or cortical bundles in the petiole of some species is not uncommon.

TABLE 1 indicates the results of a survey of the vegetative node of 25 species in 8 genera of the Magnoliaceae. These figures illustrate the extreme variability in the number of nodal bundles, not only between different species in a genus, but also between different nodes from the same specimen.

These observations do not agree, for the most part, with those of Ozenda (41), who found the nodal pattern in this family relatively stable for most genera. For purposes of comparison, Ozenda's (*loc. cit.*, p. 128) list of leaf trace numbers is as follows: *Michelia*, 3 or 5; *Liriodendron*, *Alcimandra*, and *Pachylarnax*, 7; *Talauma*, *Magnolia*, and *Manglietia*, 7 or 9; *Kmeria* and *Elmerrillia*, 9. (Apparently these numbers are exclusive of the stipular trace). The difference between these and our own observations would seem to be caused by the fact that the number of leaf traces in the Magnoliaceae varies considerably with the stage of ontogeny. For example, the first and second seedling leaves in the Magnoliaceae are vascularized by only three traces, i.e., the nodes at this stage are trilacunar. Older leaves add more traces, with the number gradually becoming more stabilized on the mature parts of the tree.

A similar variation in nodal condition was reported by Swamy (54) for *Degeneria*. Here, although the nodes of the mature stem are pentalacunar, the first few leaves of the seedling are vascularized by only three traces. In addition, large leaves from vigorously growing saplings may receive more than five traces from the corresponding node. Furthermore, numerous cases could be cited for other families which have mature trilacunar nodes but whose seedling nodes are unilacunar.

³ Ozenda (41) reports two stipular traces for *Magnolia grandiflora* L.

TABLE 1

SPECIES EXAMINED	NUMBER OF TRACES			TOTALS FOR GENUS
	MEDIAN	LATERAL	STIPULAR	
<i>Alcimandra cathcartii</i> (Hk. f. & Thoms.) Dandy	1	8	1	10
<i>Elmerrillia mollis</i> Dandy	1	12	1	
<i>E. ovalis</i> (Miq.) Dandy	1	15 *	1	14-17
<i>Kmeria duperreana</i> (Pierre) Dandy	1	7-8	1	9-10
<i>Liriodendron chinense</i> (Hemsl.) Sarg.	1	6	1	8
<i>L. tulipifera</i> L.	1	6	1	
<i>Magnolia acuminata</i> L.	1	10	1	
<i>M. coco</i> (Lour.) DC.	1	4	1	
<i>M. javanica</i> Koord. & Val.	1	6	1	
<i>M. nitida</i> W. W. Sm.	1	6	1	5-12
<i>M. salicifolia</i> Maxim.	1	3-5	1	
<i>M. virginiana</i> L.	1	6	1	
<i>Manglietia blaensis</i> Dandy	1	8	1	
<i>M. conifera</i> Dandy	1	6	1	
<i>M. hainanensis</i> Dandy	1	6	1	
<i>M. insignis</i> (Wall.) Bl.	1	7	1	8-10
<i>M. thamnodes</i> Dandy	1	6	1	
<i>Michelia baillonii</i> (Pierre) F. & G.	1	5	1	
<i>M. compressa</i> (Maxim.) Sarg.	1	4	1	
<i>M. doltsopa</i> (Buch.-Ham.) DC.	1	5	1	
<i>M. montana</i> Blume	1	6-8	1	6-10
<i>Talauma hodgsoni</i> Hk. f. & Thoms.	1	8	1	
<i>T. mutabilis</i> Blume	1	4-5	1	
<i>T. ovata</i> St. Hil.	1	6	1	
<i>T. sambuensis</i> Pittier	1	8	1	6-10

* Whenever an odd number of laterals is listed, it indicates that one bundle of a pair has been suppressed; close checks on lower sections failed to reveal its presence in these cases.

This evidence, as well as that recorded by Money et al (38) for the node of the Monimiaceae, makes it increasingly important that we reexamine Sinnott's (47) concepts concerning the phylogenetic significance of nodal anatomy. The main facts and conclusions of Sinnott (from Sinnott and Bailey, 48) are summarized as follows: 1. Three fundamental types of nodal anatomy occur — unilacunar, trilacunar, and multilacunar, depending upon the number of gaps left in the caudine stele by the departure of bundles to the leaf; 2. These three types are exceedingly constant within

the major taxonomic groups, i.e., orders and families; 3. The trilacunar type (*Text-figure 1-C*) is regarded as the most primitive, not only due to its predominance in the lower Archichlamydeae, but also because of its occurrence in the least specialized members of otherwise multi- or unilacunar families or orders; 4. The uni- and multilacunar nodes are derived from the trilacunar type respectively through a reduction series on one hand, and an amplification of lateral bundles on the other; and 5. The multilacunar node of monocotyledons has apparently been derived from such a trilacunar condition as persists in the Potamogetonaceae.

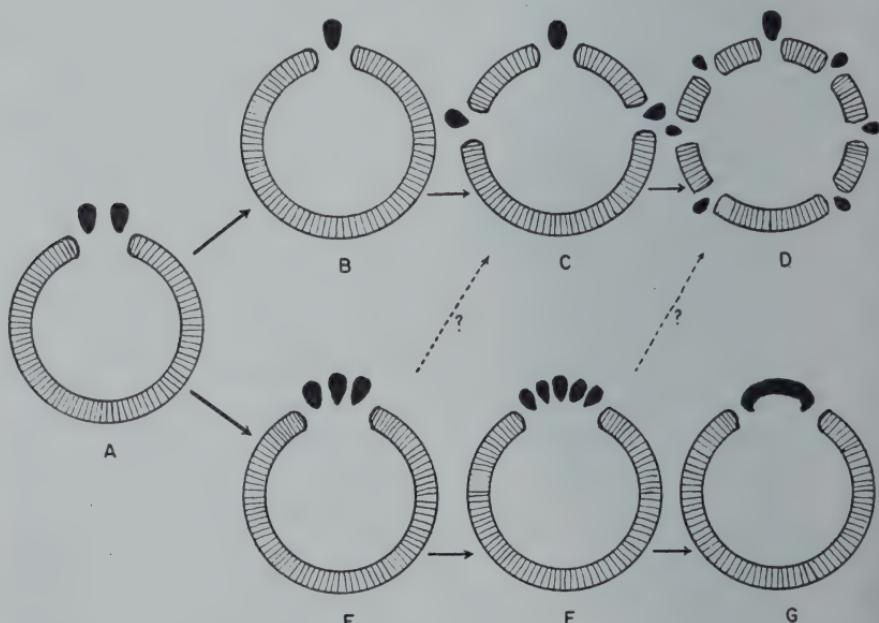
Sinnott's premises Nos. 1 and 2 are chiefly factual and have therefore become well-established and universally accepted concepts over the course of the past 40 years. On the other hand, premises Nos. 3, 4, and 5 are largely based on interpretations of the taxonomic distribution of the nodal types; it is these interpretations which are now being questioned. In other words, which of the three nodal patterns is the primitive type, and which are the derived?

Ozenda (41, p. 136) has taken the position that the three nodal types in angiosperms should be interpreted as a strict reduction series, i.e., the multilacunar type is primitive, the trilacunar or pentalacunar node is intermediate, and the unilacunar node is the most advanced. (In *Text-figure 1* this interpretation would be DCB.) Furthermore, in order to explain the occurrence of multilacunar nodes in such highly evolved groups as the Umbelliflorae, Asterales, Polygonales, etc., Ozenda has adopted the theory of *surévolution* of GausSEN (23, 24). Briefly, the basic tenets of this theory are that whenever an avowedly primitive feature is found in a plant (or animal) which is otherwise highly specialized, this apparently primitive feature is merely analogous, not homologous, to the truly primitive one, having previously passed through a complete evolutionary cycle.

However, if we are to accept the interpretation that the multilacunar node is primitive for dicotyledons, we are also forced to accept the corollary that this condition must have been inherited from either the Cycadaceae or the Monocotyledonae, the only other groups characterized by multilacunar nodes. Despite the superficial resemblance of the girdling leaf traces of the cycads to a similar condition for the lateral traces in the Magnoliaceae, *Fig. 20*, we are forced to reject any suggestion of relationship between these two groups due to a wide divergence of reproductive structures, as well as major differences in the xylem. Similarly, the fossil evidence plus the complexity of both reproductive and vegetative organs of the monocotyledons make it illogical to derive the multilacunar nodes of dicotyledons from monocotyledons. It might be mentioned in passing that Worsdell (58) attempted to derive dicotyledons from monocotyledonous plants, e.g., palms, in the belief that the "grandifoliate" habit of the latter group was a primitive feature. Little importance is attached to such a theory today.

If we reject the premise that the multilacunar node is primitive and the unilacunar node is advanced, what evidence exists which might lead us to assume that the reverse may be true?

First of all, among the lycopods, ferns, seed ferns, cordaites, ginkgos, and conifers the leaf traces are either single or double (though splitting into more in some ferns). In certain members of ancient pteropsids, e.g., *Lyginopteris*, *Mesoxylon*, *Ginkgo*, there are normally two leaf traces confronting a single gap for each leaf. No leaf gap exists in the lycopods, but a single gap occurs for the bulk of the non-angiosperm tracheophytes with the following exceptions: according to Eames (20) the node in *Ephedra* is bilacunar, although some species reportedly have two traces arising side by side; in *Welwitschia* two traces originally arise from one gap but accessory traces are added lateral to and between the original bundles as the persistent leaves widen through the years; the condition in *Gnetum* is reportedly multilacunar, 4 traces from 4 gaps (Duthie, 19) or 7-11 traces from an equal number of gaps (Sinnott, 47). Therefore, excluding



TEXT-FIGURE 1. Suggested phylogenetic trends of nodal types in angiosperms: A, two traces from a single gap represents the primitive type; B, a common unilacunar type resulting from the fusion of the two traces in the most primitive type; C, the trilacunar type resulting from an addition of two lateral traces and accompanying leaf gaps; D, a multilacunar type probably derived from the previous type by the addition of more laterals (plus a stipular trace in the case of the Magnoliaceae); E, a unilacunar type with three traces, derived from most primitive type by the splitting of one trace; F, same as E except for an increased number of traces from the single gap; G, a unilacunar type with a single broad trace derived from type F through fusion of 5-7 traces from a single gap. Thus, a unilacunar node may represent a fairly low level of specialization in the cases of types A and B, or a highly-evolved condition in the case of type G. The trilacunar and multilacunar types may, in some cases, have arisen from the unilacunar types E and F.

the highly aberrant "Chlamydosperms," it is evident that the fundamental nodal type in groups below the angiosperms on the evolutionary scale is one with a single leaf gap confronted by one or two leaf traces.

Among dicotyledons Bailey (38, p. 384) has indicated that the most common pattern of cotyledonary vascularization is one where each cotyledon is supplied by two independent traces that are related to a single gap. A strikingly similar type of vascularization has been reported by Bailey and Swamy (9) for the mature nodes of *Austrobaileya*. It is emphasized that these two leaf traces do not originate as a dichotomy of a single bundle, but instead are attached to two independent parts of the stele below the nodal level. Money et al (38) have found the same nodal condition in *Trimenia* and *Piptocalyx* (now separated out as the Trimeniaceae); the nodes of the more advanced members of the related Monimiaceae are characterized by either 3, 5, or 7 traces from a single gap, or in the case of the Siparuneae, a single broad arc-shaped trace.

Sinnott (47) has shown an ontogenetic sequence for *Chenopodium album* where the young node has three traces from a single gap, but through fusion forms a broad single trace in the mature node. Members of the Ebenaceae, Myrtaceae, and Ericaceae also show a single broad trace at the nodal level.

In summarizing the foregoing paragraphs, the following points are emphasized: 1. Nodal types in the vascular plants below the evolutionary level of the angiosperms are prevailingly unilacunar; in many cases two traces may confront a single gap; 2. In known ontogenetic sequences for certain dicotyledons (Magnoliaceae, Degeneriaceae), there is an increase in the number of leaf traces, and this tendency is usually correlated with a corresponding increase in the number of leaf gaps; 3. The basic pattern of vascularization for the majority of dicots at the level of the cotyledonary node is one with two traces from a single gap; these two traces are *not* the result of a bifurcation of a single trace further down in the hypocotyl; 4. An apparently phylogenetic sequence seen in the mature unilacunar node of the Monimiaceae (*sensu lato*) involves a series commencing with two traces (*Austrobaileya*, *Trimenia*, *Piptocalyx*), followed by types with 3, 5, or 7 traces (*Hortonia*, *Anthobembix*, *Mollinedia*), and ending with the leaf trace represented by a single broad arc (Siparuneae).

Therefore, it is suggested (See *Text-Fig. 1*) that the primitive nodal type for angiosperms is unilacunar with two traces, although these traces may sometimes be fused. By addition of laterals the trilacunar and multilacunar types evolve; these are regarded as increasing specializations of the basic unilacunar pattern. In cases of unilacunar nodes with a single broad arc of vascular tissue representing the leaf trace, this nodal type is believed to have become secondarily specialized as the end result of ontogenetic or phylogenetic fusion of several smaller traces from a single gap.

It is acknowledged that a thorough reinvestigation of the vascular pattern of both the cotyledonary and mature nodes of many widely-separated angiosperm families will be necessary before the many facets of this hypothesis can be adequately tested, and the results reliably

utilized in studies of phylogeny. Nevertheless, the present author firmly believes that sufficient evidence is now available to warrant the conclusion that the multilacunar node, as exemplified by that of the Magnoliaceae, is a highly specialized feature.⁴

Indeed, supplementary evidence of trends of evolutionary specialization from many other parts of the plant — wood, phloem, seedling anatomy, and carpels (ovules often reduced to two, and cohesion and adnation of common occurrence) — clearly indicate that the Magnoliaceae can no longer be regarded as the most primitive of angiosperms. Furthermore, the tissues and organs of the Magnoliaceae reveal many transitions between the more primitive Degeneriaceae and the slightly more specialized Himantandraceae; yet all three families undoubtedly form a compact alliance within the woody Ranales.

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EXPLANATION OF PLATES

PLATE I

FIGURES 1-7. FIG. 1. *Aromadendron elegans* Bl. (H-22787), transverse section of wood showing very large vessels, $\times 50$. FIG. 2. *Elmerrillia mollis* Dandy (H-25694), transverse section of wood illustrating large thin-walled vessels, a band of parenchyma, and secretory cells, $\times 70$. FIG. 3. *Liriodendron tulipifera* L. (H-24675), transverse section of secondary phloem showing tangential banding of sieve tube elements and phloem fibers. (Cambial zone near bottom of figure), $\times 75$. FIG. 4. *Magnolia paenetaluma* Dandy (H-21111), cross-section of wood showing small angular vessels, apotracheal narrow-banded parenchyma, and broad primary rays, $\times 75$. FIG. 5. *Alcimandra cathartica* (Hk. f. & Thoms.) Dandy (H-27724), portion of twig cross-section, $\times 75$. FIG. 6. *Kmeria duperreana* (Pierre) Dandy (H-27730), transverse section showing portion of first two growth rings, $\times 75$. FIG. 7. *Liriodendron tulipifera* L. (H-3759), transverse section of wood showing terminal parenchyma and similarity of late and early wood elements, $\times 40$.

PLATE II

FIGURES 8-19. FIG. 8. *Michelia fuscata* Bl. (H-15777), radial section showing few-barred perforation plates and spiral thickenings, $\times 100$. FIG. 9. *Magnolia cordata* Sarg. (H-8968), radial view of end of vessel element showing porous perforation resulting from loss of bars, $\times 160$. FIG. 10. *Magnolia campbellii* Hk. f. & Thoms. (H-4395L), large obliquely-oriented pore in end wall of vessel element and transitional intervacular pitting, $\times 150$. FIG. 11. *Magnolia acuminata* L. (H-17352), tangential section showing transitional intervacular pitting, fiber tracheids, and biserrate rays, $\times 65$. FIG. 12. *The same*, anomalous septations in fiber tracheids, $\times 70$. FIG. 13. *Elmerrillia ovalis* (Miq.) Dandy (Y-20574), radial view showing oil cells both in margins of rays and in strand parenchyma, $\times 35$. FIG. 14. *Magnolia paenetaluma* Dandy (H-21111), tangential section showing large number of uniseriate rays and narrow tracheid-like vessel elements, $\times 75$. FIG. 15. *Elmerrillia ovalis* (Miq.) Dandy (Y-20574), tangential section showing fairly low rays and sparse vessel distribution, $\times 35$. FIG. 16. *Aromadendron elegans* Bl. (H-22787), radial view showing scalariform vessel-ray pitting and oil cell in body of uniseriate ray of upright cells, $\times 65$. FIG. 17. *Liriodendron tulipifera* L. (H-3759), tangential view showing tyloses in vessels and nature of rays, $\times 40$. FIG. 18. *Magnolia virginiana* L. (H-8970), tangential view showing heavily-sculptured walls of wood parenchyma cells, $\times 110$. FIG. 19. *Liriodendron chinense* (Hemsl.) Sarg. (H-27731), nodal section

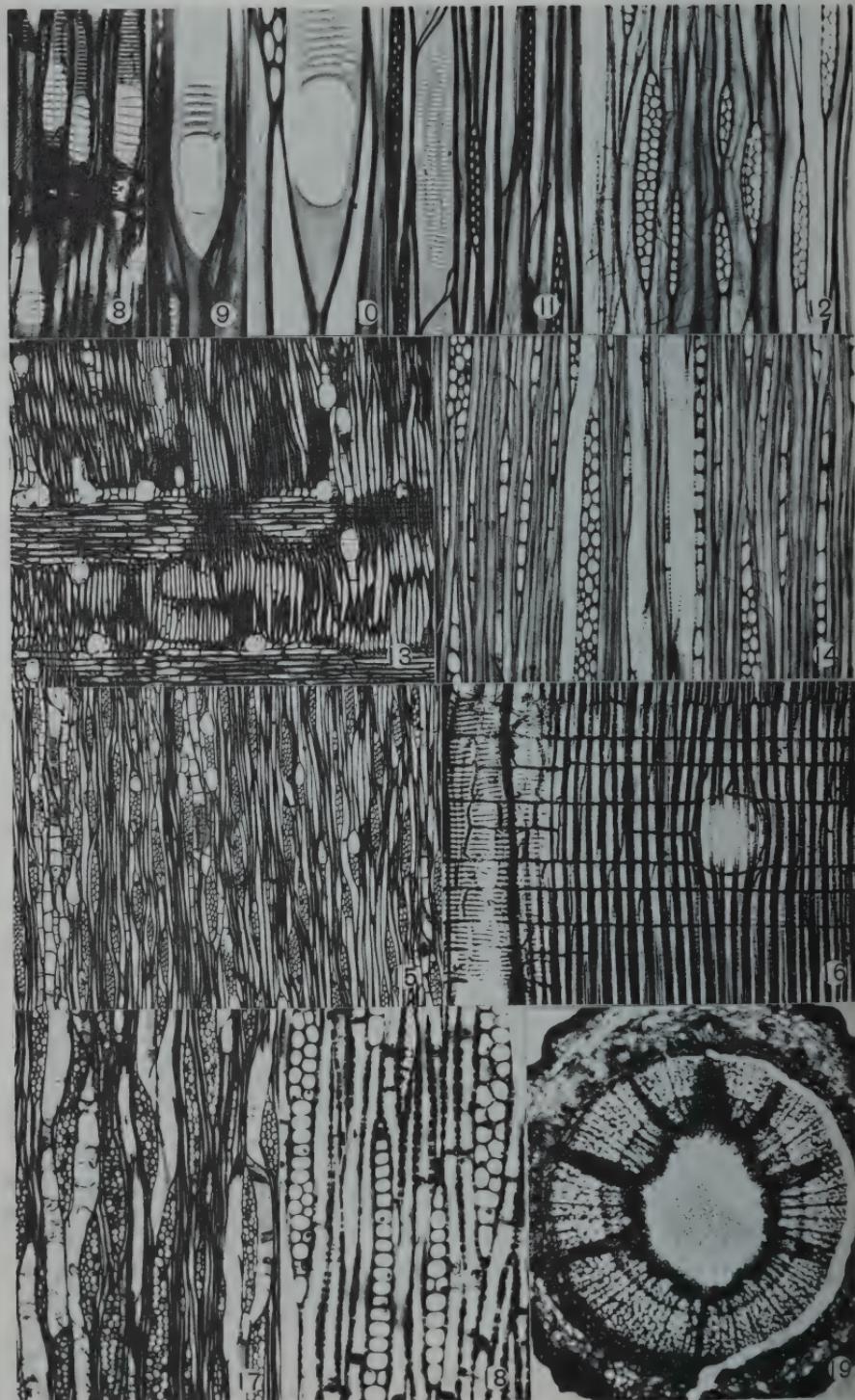
showing large median trace, three pairs of laterals, and one small stipular trace, $\times 12$.

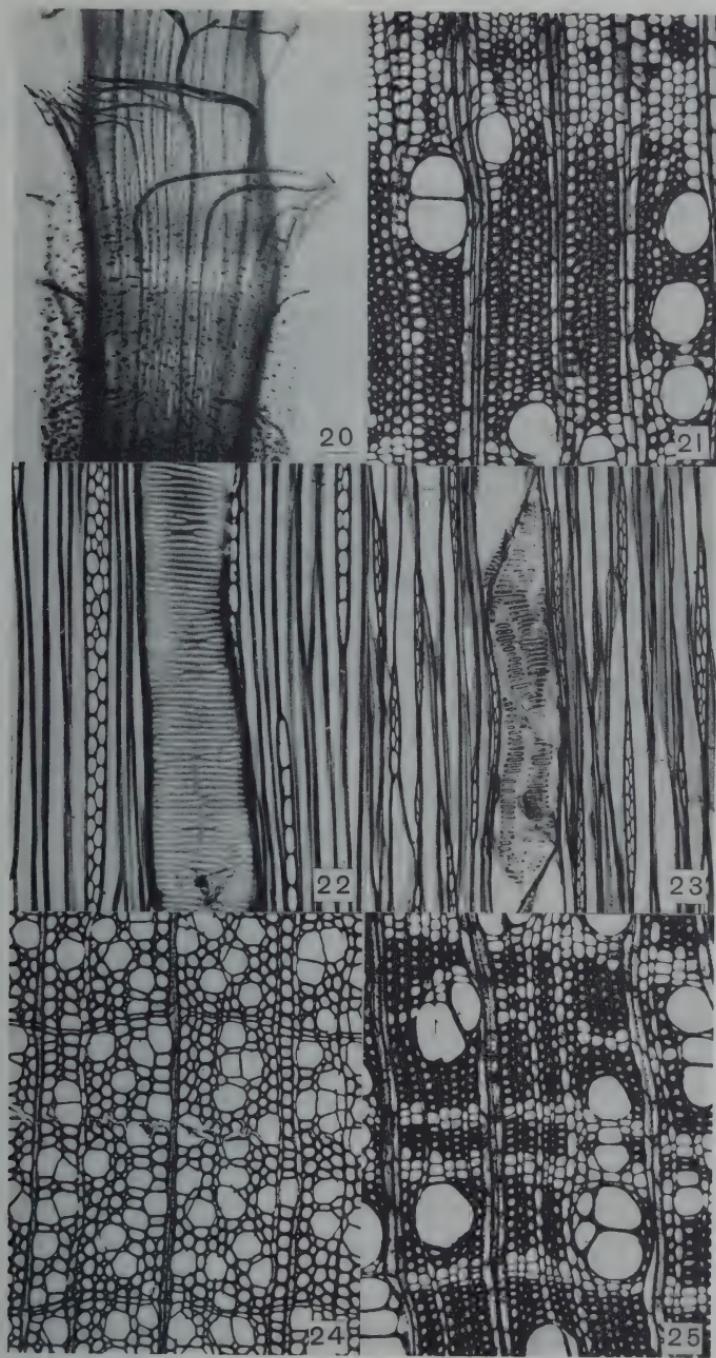
PLATE III

FIGURES 20-25. FIG. 20. *Magnolia fraseri* Walt., cleared young branch showing mode of vascularization of three spirally-arranged leaves. Dark flecks are sclereid clusters in cortex, $\times 8$. FIG. 21. *Michelia baillonii* (Pierre) F. & G. (Y-13251), transverse section of wood showing wide band of apotracheal parenchyma and some paratracheal parenchyma, $\times 70$. FIG. 22. *Aromadendron elegans* Bl. (H-22787), tangential view showing nature of intervascular pitting, $\times 85$. FIG. 23. *Manglietia glauca* Bl. (Y-30038), tangential view showing transitional intervascular pitting and narrow rays, $\times 70$. FIG. 24. *Manglietia fordiana* Oliv. (Y-31907), transverse section showing crowded angular vessels, thin-walled fiber tracheids, and two bands of terminal (?) parenchyma, $\times 70$. FIG. 25. *Talauma villariana* Rolfe (Y-17148), transverse section showing vessel distribution and numerous bands of apotracheal parenchyma, $\times 70$.



CANRIGHT, ANATOMY OF MAGNOLIACEAE





CANRIGHT, ANATOMY OF MAGNOLIACEAE

THE TAXONOMIC USE OF SPECIALIZATION OF VESSELS IN THE METAXYLEM OF GRAMINEAE, CYPERACEAE, JUNCACEAE, AND RESTIONACEAE

VERNON I. CHEADLE

With one plate

INTRODUCTION

ENOUGH PROOF of the usefulness of the vessel as a tool in phylogenetic and taxonomic studies has been given in the literature (e.g. Bailey, 1944; Cheadle, 1944; Tippo, 1946) to justify use of this measuring device in such investigations. Important studies of this nature in the dicotyledons (e.g. Bailey and Howard, 1941; Heimsch, 1942; Tippo, 1938) have been published, but with considerable emphasis on other taxonomic characters as well. If information concerning vessels in many families must always await publication only in conjunction with other available taxonomic facts, however, it is likely that such information will be extremely slow in appearing. Data of a reliable nature on secondary xylem of the stems in woody dicotyledons — such as appear, for example, in the journal *Tropical Woods* — are available for many families and there are published compendia that relate these data and other information to classification (e.g. Metcalfe and Chalk, 1950). For herbaceous dicotyledons and for monocotyledons especially, on the other hand, published information on vessels in taxa, even on the family level, is indeed scanty.

In the writer's opinion, therefore, the information at hand for families in the Monocotyledoneae should be made available for those taxonomists who may find it useful in helping to solve certain thorny questions of genetic affinity. Some examples of the possibilities of thus using the data in this report will be suggested in the DISCUSSION AND CONCLUSIONS. It seems especially pertinent to supply such information because it is now reasonably clear that vessels have arisen independently in the Monocotyledoneae (Cheadle, 1953). The vessel in the Monocotyledoneae, properly used, thus can be an independent tool — used without regard to what has happened in specialization of vessels outside the monocotyledons — in phylogenetic studies within this group of plants. If the independent origin of vessels is accepted, for example, there is no longer any advantage, each time the vessel situation in a group of monocotyledons is elucidated, in examining groups within the dicotyledons for comparable levels of specialization of vessels with the hope of suggesting, on this basis, some common relationship between the monocotyledons and dicotyledons. The modern concepts of the phylogenetic origin and specialization of vessels in the Monocotyledoneae, furthermore, were developed outside the influence of any preconceived notions (a) regarding what plants on other grounds are

considered primitive in the monocotyledons or (b) from what source the monocotyledons arose. Information on vessels in the Monocotyledoneae accordingly may be of considerable value to taxonomists, especially those interested in the monocotyledons as a whole, for use in manuals (e.g. Hutchinson, 1934) or in textbooks (e.g. Lawrence, 1951) in which phylogenetic relationships are considered.

This paper will be chiefly a report on vessels in such species as have become available up to the present in the four families Gramineae, Cyperaceae, Juncaceae, and Restionaceae. Certain of the author's information, either heretofore unpublished or not used in the same way, about the Liliaceae is also included to provide more obvious examples of the use of specialization of vessels for taxonomic purposes. Information from the Liliaceae was chosen because (a), as will be shown later, tracheary elements in this family on the average are so much less specialized than those in the four families chiefly discussed and (b) primitive members of the Liliaceae are often considered as part of the basic stock from which a number of groups of families arose (Hutchinson, 1934, p. 6). These derivatives include the four families discussed in this paper. An especially wide range of representatives of such a critical family as the Liliaceae should be investigated before tracheary elements in the family can be reliably described. Use of data from the Liliaceae in this paper, however, is such that further investigations of the family would not change the conclusions drawn. It is regrettable that for many of the species there are no herbarium vouchers, but any uncertainty concerning taxa relates only to species within genera; where there has been the slightest doubt about generic identifications,* after consultations with taxonomists, the results have been excluded. Sampling within the Gramineae and Cyperaceae is fairly representative; for the other two families many genera remain to be examined before reliable generalizations can be made. Data have been accumulated, however, for all available organs, species by species, and any one who wishes the detailed information may obtain it by corresponding with the writer.

Data from certain other families will be reported when a few more genera are examined. In the meantime, it would be helpful if plant anatomists would describe accurately the vessels in the plants—in either the monocotyledons or dicotyledons—they use for experimental or descriptive purposes, even if only a single species is involved. If the vessel turns out to be as reliable a measure of specializations as it now appears, this structure certainly should be accurately described in as many species as possible, and particularly in "critical" species where vessels could possibly serve to invalidate, or help to confirm, questionable taxonomic groupings.

MATERIALS AND METHODS

The number of species in which either roots, stems, inflorescence axes, or leaves of the plant were examined in each of the four families is shown

* Except for *Pleioblastus*.

in TABLE 1. The families are named as described by Hutchinson (1934). Where possible, Hitchcock (1951) was followed for generic names in the Gramineae and Fernald (1950) for genera in the Cyperaceae and Juncaceae. Hutchinson (1934) was followed for all other generic titles. Data from 53 species in 40 genera of the Liliaceae as understood by Hutchinson (1934) were used in establishing the place of the Liliaceae in text-figures 1-3.

The number of species studied in each genus occurs within the parentheses following each genus in the following tabulation. Totals are: Gramineae, 50 genera, 69 species; Cyperaceae, 13 genera, 36 species; Juncaceae, 2 genera, 10 species; Restionaceae, 6 genera, 12 species.

Gramineae

<i>Agropyron</i> (1)	<i>Deschampsia</i> (1)	<i>Phleum</i> (1)
<i>Agrostis</i> (1)	<i>Digitaria</i> (1)	<i>Phragmites</i> (1)
<i>Ammophila</i> (1)	<i>Echinochloa</i> (2)	<i>Phyllostachys</i> (5)
<i>Andropogon</i> (3)	<i>Glyceria</i> (4)	<i>Pleioblastus</i> (1)
<i>Anthoxanthum</i> (1)	<i>Glycerium</i> (1)	<i>Pleuropogon</i> (1)
<i>Arundinaria</i> (1)	<i>Hilaria</i> (1)	<i>Poa</i> (2)
<i>Arundo</i> (1)	<i>Holcus</i> (1)	<i>Secale</i> (1)
<i>Avena</i> (1)	<i>Hordeum</i> (1)	<i>Setaria</i> (1)
<i>Bouteloua</i> (1)	<i>Leersia</i> (1)	<i>Sorghum</i> (1)
<i>Bromus</i> (1)	<i>Lolium</i> (1)	<i>Spartina</i> (3)
<i>Calamagrostis</i> (1)	<i>Melica</i> (1)	<i>Sporobolus</i> (3)
<i>Cenchrus</i> (1)	<i>Muhlenbergia</i> (1)	<i>Thysanolaena</i> (1)
<i>Chloris</i> (1)	<i>Neyraudia</i> (1)	<i>Tripsacum</i> (1)
<i>Chusquea</i> (2)	<i>Oryzopsis</i> (1)	<i>Triticum</i> (2)
<i>Dactylis</i> (1)	<i>Panicum</i> (3)	<i>Zea</i> (1)
<i>Danthonia</i> (1)	<i>Paspalum</i> (1)	<i>Zizania</i> (1)
<i>Dendrocalamus</i> (1)	<i>Phalaris</i> (1)	

Cyperaceae

<i>Bulbostylis</i> (1)	<i>Dulichium</i> (1)	<i>Rhynchospora</i> (3)
<i>Carex</i> (9)	<i>Eleocharis</i> (4)	<i>Schoenus</i> (1)
<i>Caustis</i> (1)	<i>Eriophorum</i> (2)	<i>Scirpus</i> (4)
<i>Cladium</i> (2)	<i>Mesomelaena</i> (1)	<i>Scleria</i> (1)
<i>Cyperus</i> (6)		

Juncaceae

<i>Juncus</i> (8)	<i>Luzula</i> (2)
-------------------	-------------------

Restionaceae

<i>Anarthria</i> (1)	<i>Leptocarpus</i> (1)	<i>Lyginia</i> (2)
<i>Hypolaena</i> (2)	<i>Loxocarya</i> (4)	<i>Restio</i> (2)

Macerations were made of practically all materials using techniques described by Cheadle (1942). About three-quarters of the organs have also been sectioned. Permanent slides were prepared in all instances.

Except for the Restionaceae, most of the species were collected in and around Rhode Island. A considerable number of species is included from several other geographical areas, however, including New York, New Mexico, California, Florida, Alabama, Panama, and Australia. It is a pleasure to express thanks to all those who have supplied material. Professor A. J. Eames deserves special mention for collecting in Australia all the species studied in the Restionaceae.

OBSERVATIONS

The terms used in the following section are chiefly used as defined and illustrated in Esau (1953). For the purposes of this paper, protoxylem is considered as that area in which the tracheary elements have either annular or helical thickenings or both, metaxylem as all the remaining primary xylem. Early metaxylem is that which matures first after protoxylem and late metaxylem that which matures last (Cheadle, 1944, p. 83). Data from the shoot system were taken from the larger bundles. Small bundles need further investigation. Figures 1, 2 and 3 in Plate I illustrate the categories of metaxylem in root and shoot. Plate I, figure 7 provides examples of simple perforation plates, and figures 4-6 and 8-10 various types of scalariform plates.

The level of specialization of vessels is measured by the character of their perforation plates. The validity of this procedure has been discussed by Cheadle (1943b, p. 485). As was pointed out by the same author (1943a), specialization of the perforation plate proceeds from long scalariform plates with many bars (and perforations) on oblique end walls to simple plates (with single perforations) on transverse end walls of vessel members. Thus there is a gradation from many perforations through fewer and fewer until a single large perforation results. Scalariform perforation plates with some of their bars incompletely formed are examples of stages in this phylogenetic change; such plates frequently occur in the Cyperaceae, Juncaceae, and Restionaceae. In spite of this gradation, for ease in presentation all the degrees of specialization within the scalariform type itself have been considered as one category (scalariform). Hence the differences shown in table 1 and text-figures 1-3 are minimum differences.

Although text-figures 1-3 show the data in an easily understood fashion, they do not provide any evidence for variation in vessel specialization in each organ considered in the four families. This variation is expressed in the percentages placed in table 1 and will be discussed first.

A. VARIATION IN OCCURRENCE OF TYPES OF PERFORATION PLATES IN THE SEVERAL ORGANS

The data in table 1 demonstrate variations in the kinds of perforation plates found in the late metaxylem of the several organs of the plant in the four families under consideration. The pattern of variation in the early

metaxylem is generally comparable to that in the late metaxylem, except that it occurs at a lower average level of specialization (cf. Cheadle, 1944). While there are several important features in the table that might be discussed, the only one which needs special attention — because it is not revealed in text figures 1-3 — can be adequately treated as an answer to the following question. Are there species in each of the various families whose perforation plates are strikingly different from the average conditions in the family, and if so, in what organs do these differences occur?

If attention is turned first to the Gramineae, it is obvious that in roots, scalariform plates seldom occur and then only in company with far more

TABLE 1

PERCENTAGES OF SPECIES IN WHICH VESSEL MEMBERS WITH VARIOUS TYPES OF PERFORATION PLATES OCCUR IN THE LATE METAXYLEM OF ROOTS, STEMS, INFLORESCENCE AXES, AND LEAVES

	No. spp.	Simple only	Perforation Plates			
			Mostly simple	Simple and scalariform	Mostly scalariform	Scalariform only
Roots						
Gramineae	56	96.4	3.6	0.0	0.0	0.0
Cyperaceae	32	46.9	50.0	3.1	0.0	0.0
Juncaceae	9	55.5	22.2	11.1	11.1	0.0
Restionaceae	10	20.0	40.0	30.0	10.0	0.0
Stems						
Gramineae	69	79.7	20.3	0.0	0.0	0.0
Cyperaceae	34	8.8	82.4	2.9	0.0	5.9
Juncaceae	9	0.0	40.0	30.0	30.0	0.0
Restionaceae	12	8.3	33.4	50.0	0.0	8.3
Inflorescence						
Axes						
Gramineae	42	61.9	38.1	0.0	0.0	0.0
Cyperaceae	16	6.2	75.0	0.0	12.5	6.2
Juncaceae	8	0.0	25.0	37.5	37.5	0.0
Restionaceae	11	0.0	18.2	72.7	0.0	9.1
Leaves						
Gramineae	60	55.0	43.3	1.7	0.0	0.0
Cyperaceae	29	0.0	82.8	0.0	3.4	13.8
Juncaceae	7	0.0	14.3	14.3	57.1	14.3
Restionaceae	11	0.0	9.1	45.4	18.2	27.3

numerous simple plates. In the remainder of the plant, scalariform plates become progressively more common until in the leaves of one species (1.7 per cent) about equal numbers of simple and scalariform plates occur. As a matter of fact, under the Mostly simple column the number of scalariform plates is almost always very small; in the organs of some species only 2 or 3 were observed and these had few bars. Species in the

Gramineae obviously are so specialized in the late metaxylem that no great variation occurs.

If species in the Restionaceae are now considered, it will be seen in table 1 that their perforation plates are much less specialized than those in the Gramineae. In the roots, scalariform plates are much more numerous, and such plates become progressively more common upward in the plant until in the leaves (usually reduced to sheaths) 27.3 per cent of the species have scalariform plates exclusively.

Study of species in the Juncaceae and Cyperaceae reveals variations of a nature comparable to that in the Restionaceae; wide variations occur from species to species in some organs, less wide in others.

The occurrence of the variations being discussed is important in terms of the number of genera — or species — which should be examined before generalizations about the families can be confidently made. Where variations are within a relatively narrow range, as in the Gramineae, a smaller proportionate number of known genera should give a clear picture of specialization within the family. On the contrary, where variations occur over a relatively wide range, a greater proportion of the known genera should be examined. It is clear therefore that in the Juncaceae and Restionaceae more genera should be examined before a clear statement of their average specialization can be made. It is noteworthy, however, that the levels of evolution of the vessel within the various organs of these two families comply with the generalization made by the present author (Cheadle, 1943b, p. 489) that phylogenetically the root leads in specialization and is followed in turn by stem, inflorescence axis, and leaf. Incidentally, Gilg's (1891) and Solereder and Meyer's (1929) reports on vessels in the stems of at least 20 species in 15 genera of the Restionaceae,¹ show that in these species the variation is about equal to that found by the present writer in his material.

Table 2 is designed to demonstrate the most primitive condition of vessels, as they have been categorized in terms of perforation plates for this paper, in the various organs of the four families under discussion. This information focuses attention on the most primitive conditions of vessels in each organ of each family which must be considered when the taxonomic use of specialization of vessels is described under the section on Discussion and Conclusions. It can be understood from a glance at table 2, for example, that the most primitive category of specialization of vessels discovered thus far in the roots of any species of Gramineae is never more primitive than it is in the same organ of any species examined to date in the other families. In the remainder of the plant in the grasses, the most

¹ Fahn (1954), in a paper seen by the present author after completion of the manuscript and figures for this paper, reported tracheids in the leaf sheath of *Hypolaena fastigiata* R. Br. and "probably" tracheids in the leaf sheath of *Leptocarpus tenax* R. Br. Neither species is considered in this paper, but others in these genera are. Because bundles in leaf sheaths in the Restionaceae are probably the remnants of smaller bundles or bundle ends of typical foliage leaves, the occurrence of only tracheids does not invalidate conclusions drawn in the present paper, which are based on tracheary elements in the larger bundles.

TABLE 2.

THE MOST PRIMITIVE CATEGORIES OF VESSELS PRESENT IN THE EARLY (E) AND LATE (L) METAXYLEM OF VARIOUS ORGANS IN THE FAMILIES

	Perforation Plates									
	Simple only		Mostly simple		Simple and scalariform		Mostly scalariform		Scalariform only	
	E	L	E	L	E	L	E	L	E	L
Roots										
Gramineae					x	x ¹				
Cyperaceae			x		x					
Juncaceae							x		x	
Restionaceae						x	x			
Stems										
Gramineae	x		x							
Cyperaceae								x	x	
Juncaceae							x	x		
Restionaceae							x	x		
Inflorescence										
Axes										
Gramineae	x		x							
Cyperaceae								x	x	
Juncaceae							x	x		
Restionaceae							x	x		
Leaves										
Gramineae					x ²	x ²				
Cyperaceae								x	x	
Juncaceae							x	x		
Restionaceae							x	x		

¹ In *Zizania aquatica* L. only.² *Pleuropogon californicus* (Nees) Benth. ex. Vasey only.

primitive categories of vessels are at a much higher level of specialization than are similar categories in the remaining families. It is noteworthy that species have been found in the Cyperaceae with exclusively scalariform plates in the shoot system even though the most primitive condition for perforation plates is at a relatively high level in the roots. The significance of the information in table 2 will be brought out in the section on Discussion and Conclusions.

B. RELATIVE AVERAGE SPECIALIZATION OF VESSELS IN THE VARIOUS ORGANS OF THE FOUR FAMILIES

Text-figures 1-3 represent an attempt to give in simplified form the relative average specialization of vessels in the four families, with the Liliaceae added for comparison. To make this type of representation possible, the categories of perforation plates in the five columns of table

FIGURE 1

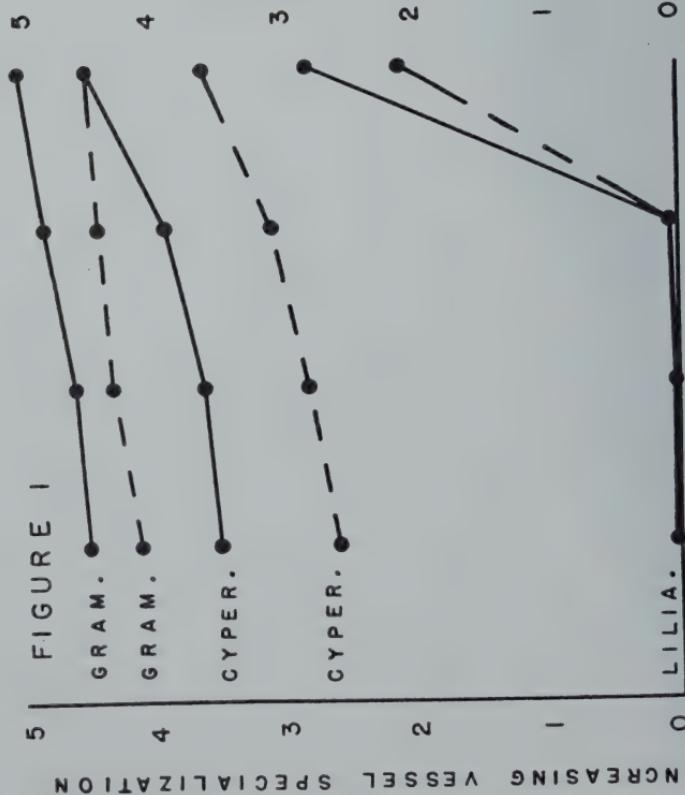
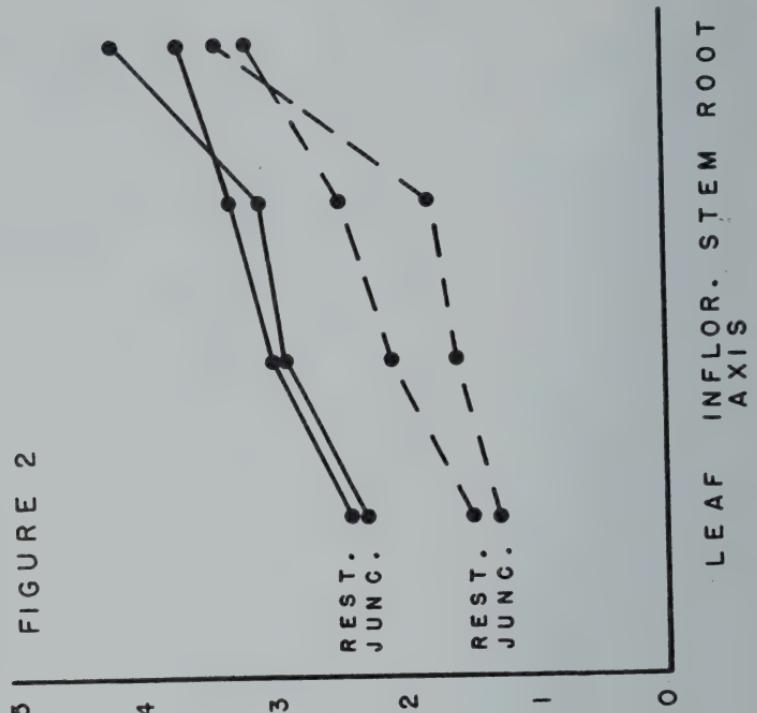


FIGURE 2



Figs. 1-2. Specialization of vessels in early (dashed line — roots only in Liliaceae) and late (solid lines) metaxylem in various organs of Gramineae, Cyperaceae, Juncaceae, Restionaceae, and Liliaceae. (Use of numbers described in text.)

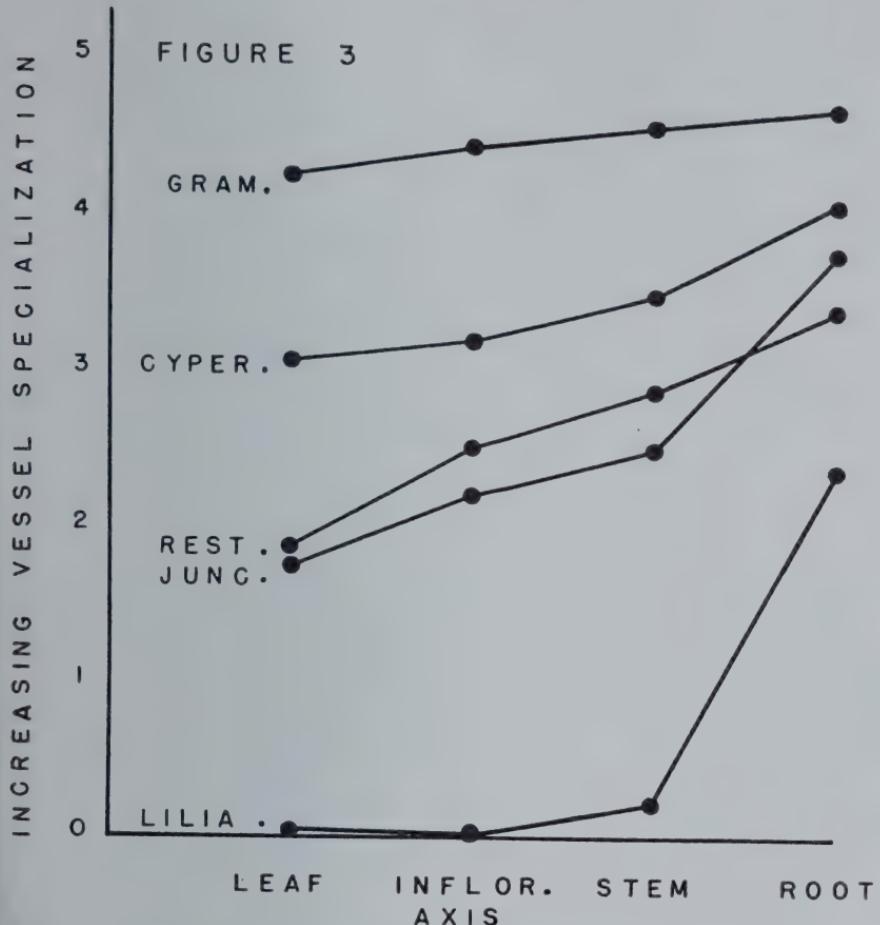


FIG. 3. Specialization of vessels in entire metaxylem in various organs of Gramineae, Cyperaceae, Juncaceae, Restionaceae, and Liliaceae. (Use of numbers described in text.)

I have been arbitrarily assigned the following numerical values of specialization: scalariform only — 1, mostly scalariform — 2, simple and scalariform — 3, mostly simple — 4, simple only — 5. To make possible the inclusion of the Liliaceae, whose species generally have only tracheids in the shoot system, tracheids are valued at 0. Numerical values for each organ in every species were assigned to vessels or tracheids in both early and late metaxylem. These numbers were then averaged and the values thus obtained were used in making the graphical representation of specialization. Values for vessels in early and late metaxylem were averaged separately for text-figures 1 and 2. (The differences between these areas were so small in the shoot system of the Liliaceae that the early metaxylem is shown only for roots.) The average for all metaxylem in text-figure 3

was obtained by simply averaging the averages for early and late metaxylem. Lines are drawn from organ to organ in each family only to provide easier reference to values for such organs in the same family. Average values for all organs in one family were not used because of the wide differences, except for the Gramineae, usually shown in specialization of vessels in various organs of the same family.

This representation of the data makes it possible to note at a glance the average specialization of the vessels throughout the various organs of the plant in a given family and to compare the families organ by organ.

Two important features in text-figures 1 and 2 need discussion. One conclusion to be drawn from text-figures 1 and 2 is that in every organ the late metaxylem, on the average, is more highly specialized in terms of perforation plates than is the early metaxylem. It is obvious therefore that differences in specialization of vessels between any two families should not be measured between the early metaxylem in one family and the late metaxylem in the other. Such differences can be shown realistically, however, by comparing data from either early or late metaxylem or averages of the data from both late and early metaxylem. A second point of importance to be drawn from a study of text-figures 1 and 2 is that, within the same family, the metaxylem on the average differs from organ to organ in degrees of specialization, as measured by types of perforation plates present. As pointed out earlier, the root leads in specialization of vessels and is followed by stem, inflorescence axis, and leaf. Thus, for the most meaningful comparison of families, the average condition should be compared organ by organ. It follows that information in the literature on vessels which does not provide accurate observations in terms of organs, and of early and late metaxylem within the organs, cannot be used for studies of the present type, because such information is apt to be misleading in any event and may be useless when differences between families are small.

Several aspects of text-figure 3, which represents the average specialization of vessels in the metaxylem as a whole in various organs of the families, should be emphasized. (1) The high degree of specialization of the grasses is evident. Specialization of vessels in the leaves of the Gramineae, for example, has reached a point higher than that for vessels even in the roots of the Cyperaceae, in specialization the nearest rival to the Gramineae among the families represented in the figure. (2) Vessels have reached about the same level of specialization in the Juncaceae and Restionaceae, although those in the roots of the Juncaceae seem notably more specialized than those in the remainder of the plant in that family. (3) Vessels in the roots of the species of Liliaceae examined have reached a fairly high stage of specialization on the average, in spite of the fact that vessels are uncommon (and invariably primitive) throughout the shoot system. Variation in specialization of perforation plates in the roots of various species in the Liliaceae, however, runs through all gradations from the occurrence of (a) extremely primitive scalariform plates in the late metaxylem together with tracheids in the earliest metaxylem, to (b)

simple plates throughout the metaxylem. (4) Average specialization of vessels in the roots of the Liliaceae has surpassed that of vessels in leaves of the Juncaceae and Restionaceae and is comparable to that in both the inflorescence axes and stems of the Juncaceae and that in the inflorescence axes of the Restionaceae. (5) Organ for organ, the averages of specialization of vessels in the Juncaceae, Restionaceae, Cyperaceae, and Gramineae are above those of vessels in the Liliaceae. The greatest differences usually lie in comparisons of the leaves, the least differences reside in comparisons of the roots. (6) On the basis of increasing specialization of vessels, organ for organ, the families fall into the sequence Liliaceae, Juncaceae and Restionaceae, Cyperaceae, and Gramineae.

It is obvious from a consideration of text-figure 3 that some of the families differ markedly from one another in the average specialization of vessels and that others differ very little. The possible taxonomic use to which these differences can be put will be discussed in the next section.

DISCUSSION AND CONCLUSIONS

In dealing with data that are susceptible of interpretation in the form of salient trends of phylogenetic change, there is always the possibility that the data are too few or too unrepresentative to form a reliable source of information. One is constantly haunted, for example, by the possibility that accumulation of new data from larger numbers of species or from species from additional geographical areas over the world, or from additional environmental niches, might make necessary a substantial revision of our conclusions about the principal trends of evolution of vessels, even though such conclusions were induced originally from a considerable body of evidence. The present author has met this compulsion for additional evidence by continually adding to the body of data available for study of vessels. For example, although not all are included in the present paper, data from an additional 36 species of 25 genera in 7 families (one heretofore unavailable) have been considered since the last publication (Cheadle, 1953, p. 38) on vessels in the Monocotyledoneae. The total representation of the Monocotyledoneae is now 428 species in 274 genera of 42 families (as defined by Hutchinson, 1934). From all the additional 108 species (including those in 7 new families) that have been examined since the original publication on the origin and trends of specialization of vessels in the monocotyledons (Cheadle, 1943a), there has not come a single new observation to contradict the general statements made in that paper concerning phylogenetic changes in tracheary elements. This does not mean, of course, that such facts may not yet be discovered as a wider and wider representation of monocotyledons is subjected to study. Nevertheless, it becomes increasingly evident that the origin and specialization of vessels represent a series of evolutionary changes of perhaps unparalleled clarity in the monocotyledons (and in vascular plants generally, Bailey, 1953, p. 6).

In spite of the clarity with which the evolutionary development of

vessels in the monocotyledons can be described, the use of specialization of vessels to the taxonomist is limited. For example, within the Gramineae, the range of variation in specialization is so small that reliable measures of the differences in many instances are hardly possible and in any event would be impractical to ascertain for use in typical taxonomic descriptions. It can be reported, on the other hand, that only two (*Cladium mariscoides* (Muhl.) Torr. and *C. jamaicense* Crantz, as named in Fernald, 1950, p. 290) of the 36 species examined in the Cyperaceae have scalariform plates exclusively throughout the shoot system. Further investigation may prove that these species could be set apart, for purposes of identification, from the remaining members of the family on this basis alone. For the most part, however, information on vessels in terms of such use needs to be much more complete. Yet even in the absence of a more complete record, there seems to be justification for employment of tracheary elements as one of the factors in the determination of phylogenetic relationships of taxa within the monocotyledons. In some situations, the taxa may be species, in others genera, or tribes, or families, or even orders; the possible latitude can be determined only by further investigations.

If it is granted that tracheary elements are possible tools for use in developing phylogenetic relationships of members of the Monocotyledoneae, it should also be made clear that there are specific pitfalls to be wary of and a necessary body of knowledge to be acquainted with. Some of these matters were mentioned in the preceding section on *OBSERVATIONS*, but they are also included here for emphasis. (1) Tracheids are more primitive than any vessels. (2) Although scalariform perforation plates of any type are more primitive than simple perforation plates, those with few bars are more specialized than those with many bars. (3) Where readily identifiable variation occurs throughout the plant, taxa must be compared organ for organ. For example, vessels in roots of some species may have exclusively simple perforation plates before vessels appear in any part of the shoot system (*Aloe*), or in a given species specialization of vessels may be at the same low level (*Pandanus*) or at the same high level (many species of grasses) throughout the plant. (4) There is no real evidence of reversibility in the phylogenetic series from tracheids to highly specialized vessels, particularly as measured by the perforation plate. One possibility of misinterpreting observations as evidence for such reversibility in tracheary elements concerns congested areas in the plant, such as nodes, or slow growing rhizomes. Crowding of tracheary elements in congested areas may appear to reduce numbers of bars in scalariform plates and thus to illustrate phylogenetic reversibility. When such areas are properly evaluated in terms of a broad sampling, however, it will be found that physical crowding simply prevents the formation of elongate end walls, either by tracheids or vessel members, and thus large numbers of bars do not occur in perforation plates in such areas whether or not they occur elsewhere in the plant. The small number of bars can not be considered as reduction, for large numbers were never present in such areas; that is, the evolutionary series starts with short elements (tracheids)

in the first place and long end walls were never present in the phylogenetic change to vessels. As a matter of fact, lateral conduction may be emphasized in such congested areas, for perforation plates frequently occur on the lateral walls of vessel members. (5) It must be emphasized, as Bailey (1944, p. 425) has done, that specialization of vessels is chiefly reliable as evidence in "negations" of putative phylogenetic relationships. This point of view is based (a) on the conclusion that specialization of vessels is irreversible and (b) on the assumption that no other evolutionary series is so well founded on observable facts in extant or extinct plants. An illustration of the application of this approach to phylogenetic relationships is negation of the possibility that the Liliaceae arose from any extant members of the Butomaceae having simple perforation plates in their roots. Such an origin actually may seem reasonable in relation to the gynoecium, for example, but there are species in the Liliaceae having the most primitive types of scalariform plates on vessel members in the late metaxylem of the roots which negate such an origin for the Liliaceae. (7) From a positive point of view, specialization of vessels can offer only suggested relationships, which must be borne out by the weight of other evidence. In this connection, one must not overlook the possibility that even though in a family vessels may have reached a high average degree of specialization, the occurrence in it of species with very primitive vessels may preclude a possible origin of this family from another family in which the average specialization of vessels is relatively low, but in which no species with really primitive vessels occur. An illustration of this statement occurs in point 3 in the following paragraph.

Keeping in mind the enumerated statements just made, the observations noted earlier in the paper, table 2, and text-figure 3, some examples of the use of specialization of vessels in determining possible phylogenetic relationships as they concern the Gramineae, Cyperaceae, Juncaceae, Restionaceae, and Liliaceae, as now known, can be enumerated. It should be emphasized that especially points 3, 4, and 5 below are tentative statements and that their validity must be checked by study of more representatives of the families Restionaceae and Juncaceae. One now knows, however, what critical stages of specialization of vessels to look for in any new materials of these families. (1) The Gramineae, as known from investigations up to date, could not have given rise to any of the other four families represented in text-figure 3, because vessels in all species of the grasses have already reached too high a degree of specialization. (2) The general average of specialization of vessels in the Cyperaceae is rather high, but there are two species [*Cladium mariscoides* (Muhl.) Torr. and *C. jamaicense* Crantz] whose vessels in the shoot systems are as primitive, or more primitive, than those in species of the Restionaceae or Juncaceae. In the roots of these two species, however, the vessels are more specialized than are vessels in the same organs in some members of the Restionaceae or Juncaceae. The Cyperaceae, on the basis of present knowledge, thus can not serve as a source of the Juncaceae or Restionaceae. (3) No species examined to date in the Juncaceae has vessels quite primitive enough

throughout the plant to permit use of the Juncaceae as the source of the most primitive members of the Cyperaceae or of the Restionaceae. (4) Vessels of one species in the Restionaceae (*Lyginia* sp.) are primitive enough to make possible the origin of the most primitive members of the Cyperaceae from the Restionaceae. (5) In spite of the primitive vessels throughout the shoot system of one species in the Restionaceae (*Lyginia* sp.), vessels in the roots of that species are not primitive enough to make possible the origin of the most primitive members of the Juncaceae from the Restionaceae. (6) Numerous species in the Cyperaceae, Restionaceae, and Juncaceae have vessels throughout the plant primitive enough to make possible the origin of the most primitive members of the Gramineae from any of these families. (7) There is no possibility of deriving the Liliaceae from the Juncaceae, Cyperaceae, Restionaceae, or Gramineae because all species in these four families have vessels throughout the plant and most species in the Liliaceae lack vessels throughout the shoot system. (8) Although a few species in the Liliaceae have vessels throughout the plant, all these have exclusively the most primitive types of vessels in the shoot system. Vessels in the shoot system of the Juncaceae, often thought to be closely related to and derived from the Liliaceae (Hutchinson, 1934, p. 187) are more specialized. This derivation of the Juncaceae, even from some of those species in the Liliaceae having vessels in the shoot system, therefore is supported by the relative specialization of vessels in the two families. (9) Although the Juncaceae may have been derived from the Liliaceae, as understood by Hutchinson (1934), vessels in the roots of a number of species of the Liliaceae (e.g. all investigated species of *Aloe*, *Asparagus*, *Johnsonia*, *Paradesia*) preclude involvement of these species in this derivation, because these vessels are already more highly specialized than those that occur in the roots of some species in the Juncaceae. (10) On the same basis as noted above for the Juncaceae, except for minor differences in detail, the Cyperaceae, Restionaceae, and Gramineae could all have been derived from the Liliaceae.

These enumerated statements provide examples of the possible uses of the absence of, and when present the specialization of, vessels in the various organs of the plants in the Monocotyledoneae. It is obvious that the more complete the representation of examined species the more useful the information on vessels will be. Additional information accordingly will be made available from time to time as it is collected. Meanwhile, the author's more detailed information on species already studied is available to anyone who has good use for it.

SUMMARY

1. The average specialization of vessels in the metaxylem of the Gramineae, Cyperaceae, Juncaceae, and Restionaceae is described; that of the Liliaceae is considered for contrast. On the basis of specialization of vessels, the Gramineae rank highest and are followed in turn by the Cyperaceae, Juncaceae and Restionaceae, and Liliaceae.

2. The most primitive condition found in any species in each family is given, together with the variation of specialization of vessels in every organ in all families.

3. The clarity and the irreversibility of the phylogenetic trends in the origin and specialization of vessels in the Monocotyledoneae are discussed in terms of using variations in specialization of vessels to help determine certain possibilities of phylogenetic relationships of the families described.

4. After limitations and necessary qualifications in the use of specialization of vessels in phylogenetic studies of taxa are reviewed, suggested examples of this use are provided. Among the more important of these, in the light of our present knowledge, are: The Gramineae can not be the source of any of the remaining families, but the converse is true. The Juncaceae and Restionaceae can not be derived from the Cyperaceae. The Cyperaceae can be derived from the Restionaceae, but not from the Juncaceae, in so far as they have now been examined. On the basis of available evidence, the Juncaceae and Restionaceae can not be derived from each other. The two preceding statements are actually tentative, and further material is needed to test their validity. The Liliaceae can not be derived from any of the other four families, but all four can be derived from the Liliaceae; yet there are many existing species in the Liliaceae which could not have taken part in this derivation.

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EXPLANATION OF PLATE I

FIG. 1. *Pleioblastus argenteostriatus* (Regel) Nakai (Gramineae). Transverse section of vascular bundle from stem, showing two large vessels (LM) of late metaxylem and smaller vessels (EM) in early metaxylem. $\times 131$.

FIG. 2. *Pleioblastus argenteostriatus* (Regel) Nakai (Gramineae). Transverse section of portion of root, depicting vessels in late metaxylem (LM) and vessels in early metaxylem (EM), together with sieve tubes (S) not in the customary phloem position. The tiny, thin-walled cells (PH) represent the phloem strands in typical peripheral position. $\times 148$.

FIG. 3. *Cyperus filiculmis* Vahl (Cyperaceae). Transverse section of bundle from stem, showing two vessels in late metaxylem (LM) and the early metaxylem area (arrow from EM). The letters EM are actually placed in the protoxylem lacuna. $\times 420$.

FIG. 4. *Cladium mariscoides* (Muhl.) Torr. (Cyperaceae). Longitudinal section of stem, showing vessel members with end walls in section. Relatively small number of perforations occurs in the long end walls of vessel members. Imperforate pits occur in the upper half of the end walls. $\times 420$.

FIG. 5. *Cladium mariscoides* (Muhl.) Torr. (Cyperaceae). From same section as in Fig. 4, but with vessel members having longer end walls and greater number of perforations. Note thinner bars in center of end walls. $\times 420$.

FIG. 6. *Carex lurida* Wahlenb. (Cyperaceae). Longitudinal section of stem, showing vessel members with their oblique end walls cut on bias. Branching of bars and variation in size of perforations (areas between bars) are evident. $\times 258$.

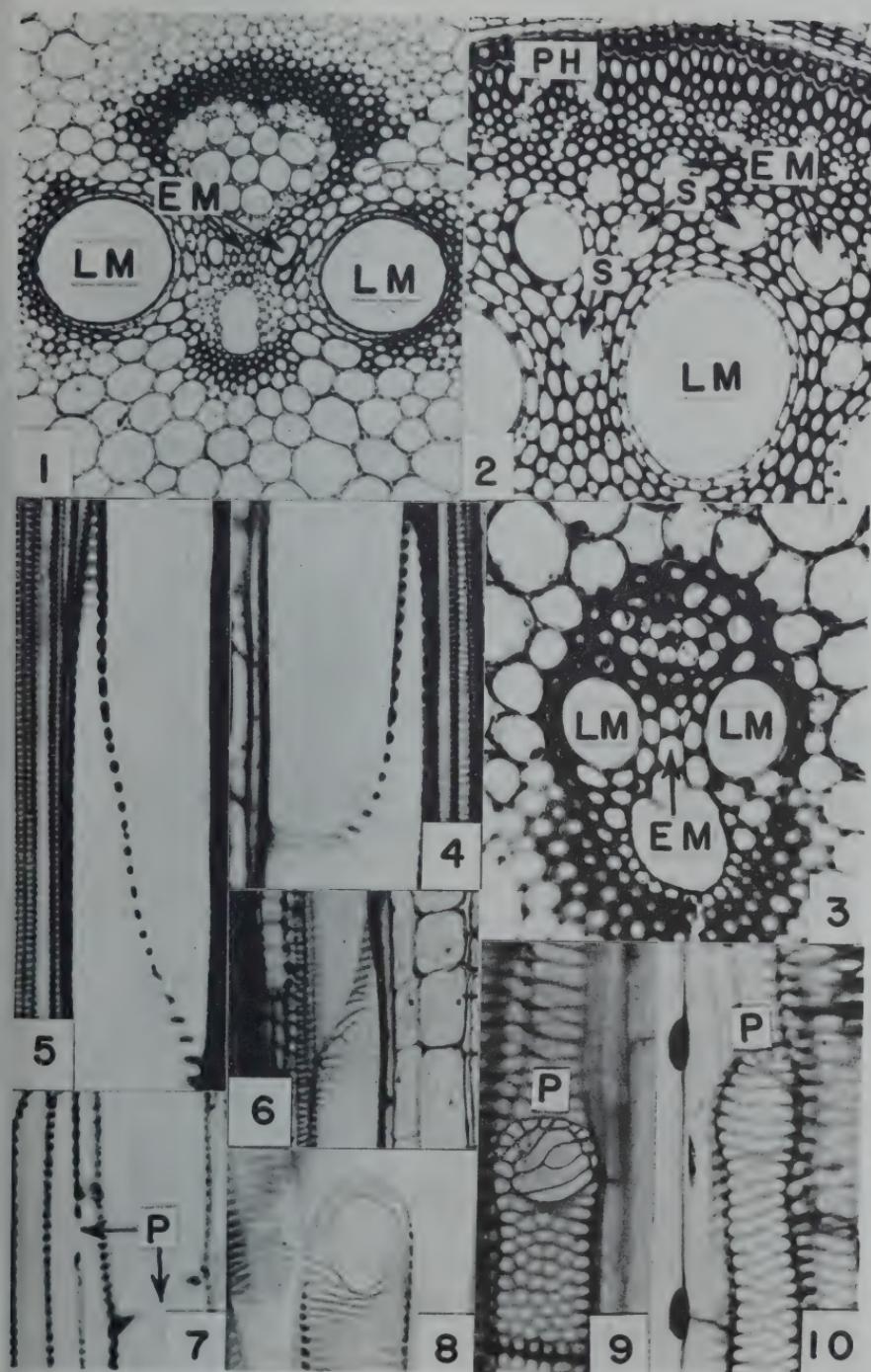
FIG. 7. *Arundo donax* L. (Gramineae). Longitudinal section of bundle from

leaf, illustrating simple perforation (P) in end walls of large vessel members in late metaxylem and one on side walls of small vessel members in early metaxylem. $\times 510$.

FIG. 8. *Carex intumescens* Rudge (Cyperaceae). Separated vessel element from stem, illustrating simple perforation with remnant of bar discernible at right. Remnants of varying number frequently occur in perforation plates of vessel members in some species of Cyperaceae, Juncaceae, and Restionaceae. $\times 578$.

FIG. 9. *Zea mays* L. (Gramineae). Longitudinal section of stem, showing small branched scalariform plate (retouched) — just below P — in side wall of vessel member in early metaxylem. Only large pits are perforate; the smaller ones (sides and top) are imperforate. $\times 510$.

FIG. 10. *Zea mays* L. (Gramineae). From same section as in FIG. 9, but vessel member with more typical scalariform plate (just below P) on lower two-thirds of end wall. Reticulate wall thickening evident on side wall in face view. $\times 510$.



CHEADLE, SPECIALIZATION OF VESSELS

THE POLLEN MORPHOLOGY OF SEVERAL GENERA EXCLUDED FROM THE FAMILY ICACINACEAE

A. ORVILLE DAHL

With one plate

THE FAMILY ICACINACEAE MIERS. has been investigated in detail in recent years with respect to secondary xylem (*cf.* Bailey & Howard, 1) and pollen (Dahl, 2). During the analysis of pollen of all of the available genera, pollen material of several genera either assigned with some question to the Icacinaceae or believed to have possible alliances with this family were examined. These include the following: *Pseudobotrys*, *Lophopyxis*, *Pteleocarpa*, *Metteniusa* (*Aveledoa*), *Peripterygium* and *Trichadenia*. Some authors have recommended that some of these genera be excluded from the Icacinaceae (*cf.* Howard, 5 and 6 and Sleumer, 7). In view of these circumstances, a summary of the pollen characters occurring in this material seems in order in terms of possible clues concerning the natural relationships of the entities involved. Reference to detailed data and figures will make it evident that each of the species is distinct from the standpoint of pollen morphology.

To Professor I. W. Bailey, I am very grateful for most of the pollen specimens examined. Dr. H. Sleumer kindly called my attention to specimens of *Metteniusa tessmanniana* in the herbarium of the New York Botanical Gardens. I am indebted to Dr. David Keck for the recent loan of this material.

All of the observations as herein reported are based upon pollen derived from herbarium specimens. (The letter A refers to specimens from the Herbarium of the Arnold Arboretum while NY refers to those from the New York Botanical Gardens.) The preparational procedure for the lactic acid mounts has been previously summarized (2). The figures, while completed in semi-diagrammatic form, are based upon drawings of individual grains made with camera lucida. An apochromatic objective (90X, N.A. 1.3) and compensating oculars (12X) were used for observation. Miss Wilma Monserud has kindly prepared the illustrations. Data on pollen grain size refer, respectively, to length and diameter.

The chief diagnostic characters of the pollen of the seven entities analyzed are given below. Most of the descriptive terms used follow the applications presented by Faegri and Iversen (4) and Erdtman (3).

1. PSEUDOBOTRYS MOES.

Pollen grains oblate; triaperturate; large, bulging elliptical apertures; possibly tricolporate since a depression or fold extends from the aperture

in direction of the poles; exine foveate to foveolate; in the immediate vicinity of the aperture, a region of exine (to the radial extent of ca. 3-4.5 μ) is very thin thereby contributing to an ascending or protruding character of the aperture.

Pseudobotrys cauliflora (Pulle) Sleumer. — FIGS. 1, 1A. — 54.3 \times 62.4 μ . — *Brass 7005* (A).

2. LOPHOPYXIS HOOK. F

Grains ellipsoidal; tricolporate; furrows constricted at the equator, obscuring the germ pore; pore circular to somewhat oblong (long axis parallel to the equator) in outline; exine conspicuously foveate with many of the foveae of elliptical outline.

Lophopyxis pentaptera Engl. — FIGS. 2, 2A. — 38.9 \times 30.2 μ . — Collector unknown 1775 (A).

3. PTELEOCARPA OLIV.

Grains spheroidal to ellipsoidal; tricolporate as in *Lophopyxis*; furrows constricted over the germ pore; exine foveate, very much as in *Lophopyxis*.

Pteleocarpa malaccensis Oliv. — 37.0 \times 32.0 μ . — *Maingay* (A).

4. METTENIUSA KARSTEN (INCLUDING *Aveledoa* PITTIER)

Pollen grains ellipsoidal; triangular in polar view because of the domed or vestibulate character of the germ pore region; tricolporate with distinct, usually bulging germ pores of more or less rectangular outline (see FIGS. 3A and 4A); frequently small granules of exine occur on the pore and furrow membranes; exine, while almost smooth in outline in its general effect, possesses a distinctive complexity in its fine structure; in polar regions the exine is foveolate-foveate; as one proceeds to equatorial regions there is a transition to a delicately rugulate character that finally is supplanted by a finely areolate-verrucate surface, particularly in the region of the equator; in the vicinity of the furrows the exine is foveolate. It should be noted in FIGS. 3 through 4A that the various exine structures (foveae and areolae) are presented in outline only because of their small dimensions.

Metteniusa nucifera (Pittier) Sleumer. — FIGS. 3, 3A. — 42.0 \times 40.8 μ . — *A. Jahn* 1202, CO-TYPE (NY).

As in the following species the furrows are well-defined with minute irregularities in the margin. Occasionally the furrow is constricted over the germ pore (FIG. 3A).

Metteniusa tessmanniana (Sleumer) Sleumer. — FIGS. 4, 4A. — 42.8 \times 39.7 μ . — *G. Tessmann* probably 4042, TYPE (NY); *G. Tessmann* 4235 (NY).

Within the genus, the areolate-verrucate character of the exine was most conspicuously developed in 4235.

5. PERIPTYGYIUM HASSK. (? *Cardiopteris* WALL.)

Grains oblate; triangular in polar view; tricolporate; furrows narrowly tapering and extending almost to the more or less flattened poles; exine foveolate with the exception of the polar regions; foveolae are noticeably aligned radially giving a locally striate effect.

Periptygium moluccanum (Blume) Sleumer. — $10.7 \times 16.3 \mu$ — Collector unknown 38579 (A).

6. TRICHADENIA THW.

Grains spheroidal; tricolporate with long, tapering well-differentiated furrows; in direction of the poles, the circular germ pore is sometimes bounded by small club-shaped elements (pilae or clavae); exine conspicuously clavate; the pilae while polymorphic are largely dimorphic, *i.e.* of two size classes; the pilae of small size have a diameter (head) of ca. 0.7μ while those of large size are 1.5 to 3.2μ in diameter; the large elements are scattered over the surface imparting a striking warty appearance to the grain.

Trichadenia philippensis Merr. — 28.7μ (diameter) — Phil. Bur. Sci. 2982 (A).

DISCUSSION

None of the pollen complexes described above agrees entirely with the highly distinctive patterns of pollen morphology occurring in a number of representatives within the family Icacinaceae. However less specialized foveate, triaperturate types of pollen occur in a number of species within the Icacinaceae. Such types are also found in a number of other families. Of the genera discussed here, only *Pseudobotrys* and *Lophopyxis* in their pollen morphology have some, but not marked, similarity to certain genera in the Icacinaceae. For example, *Leptaulus* has some features of *Pseudobotrys* while *Icacina*, *Lavigeria*, and *Leretia* exhibit some characters of *Lophopyxis*. However, the pollen morphology of the investigated preparations does not suggest their inclusion within the Icacinaceae as presently defined. Their affinities on the basis of pollen alone are, naturally, difficult to sense.

The placing of *Pteleocarpa* in the Boraginaceae is not supported by pollen morphology. Indeed it should be noted that pollen of the specimen labelled "*P. malaccensis* Oliv." is identical with that of *Lophopyxis*. Further, the suggestion that *Pteleocarpa* be assigned to *Periptygium* is not verified by the pollen preparation. The genus *Lophopyxis* would appear to be its rightful assignment. It is relevant also to note that the range of pollen forms known to exist within the family Euphorbiaceae could include that of *Lophopyxis* (see Erdtman).

Periptygium has been assigned to the family Periptygiaceae. Slight

similarity in size and apertures of the pollen grains of *Peripterygium* to those of *Coula* in the Olacaceae has been reported by Erdtman (3).

The various affinities of *Metteniusa* cannot be stated here with certainty. Sleumer (7) assigns this genus to the tribe Icacineae of the Icacinaceae whereas Howard (5) suggests its exclusion from the family. While the pollen of *Metteniusa* possesses some of the wide-spread characters seen in many families including the genera within the Icacinaceae having Type A pollen (2), it does not agree in its distinctive complex of characters with any of the individual examples of pollen within the Icacinaceae. For example, the pollen of *Metteniusa* differs in number and structure of the germinal apertures from *Alsodeiopsis* and in structure of the germinal apertures from *Merrilliodendron*. It will follow that its inclusion within the family Icacinaceae would represent the addition of a new combination of pollen characters. Howard (5) has reported, also, that in a number of its floral (corolla, stamen, and pedicel) characters it finds no counterpart, in so far as presently known, within the family.

The suggestion that *Metteniusa* has alliance with the Convolvulaceae is not confirmed by pollen morphology. The pollen grains of *Maripa* and *Erycibe*, for example, are typically convolvulaceous and markedly differentiated from those of *Metteniusa*.

The assignment of *Metteniusa* to the family Boraginaceae near the genus *Cordia* seems inappropriate on the basis of pollen characters. *Cordia gerascanthus* L., for example, produces entirely distinct echinate, oblate spheroidal, tricolporate pollen grains.

Thus far, I have no pollen evidence clearly relating *Metteniusa* to the several pollen types included within the Olacaceae. An illustration of the distinctly different pollen form is seen in *Olax scandens* Roxb. and *O. triplinervis* Oliv. where the triporate pollen grains are psilate and oblate (see also Erdtman, 3, for other examples).

In its unusually distinctive pollen grain, *Trichadenia* is somewhat suggestive of *Ilex* in the Aquifoliaceae. However the marked dimorphism of the pilae in *Trichadenia* is not seen in *Ilex verticillata* Gray where the pilae or clavae are relatively more uniform and of small size. The inclusion of *Trichadenia* in the family Flacourtiaceae gains support from an examination of pollen of another genus in this family, namely in *Samyda grandiflora* Griseb. where the tricolporate pollen grains exhibit a suggestively similar warty surface.

From the above analysis of the available pollen material, one may conclude that a number of these entities do not exhibit typically icacinaceous pollen characters. Until a larger complex of various characters can be fitted together, the more or less detailed affinities of some of these genera largely remain a problem for the future. In a number of instances, however, the data on pollen suggest the possible relationships which are worthy of serious consideration.

SUMMARY

1. Descriptions are provided summarizing the pollen morphology of species assigned to the genera: — *Pseudobotrys*, *Lophopyxis*, *Pteleocarpa*, *Metteniusa*, *Peripterygium*, and *Trichadenia*.

2. The possible affinities of these entities are discussed in terms of known patterns of pollen form.

DEPARTMENT OF BOTANY,
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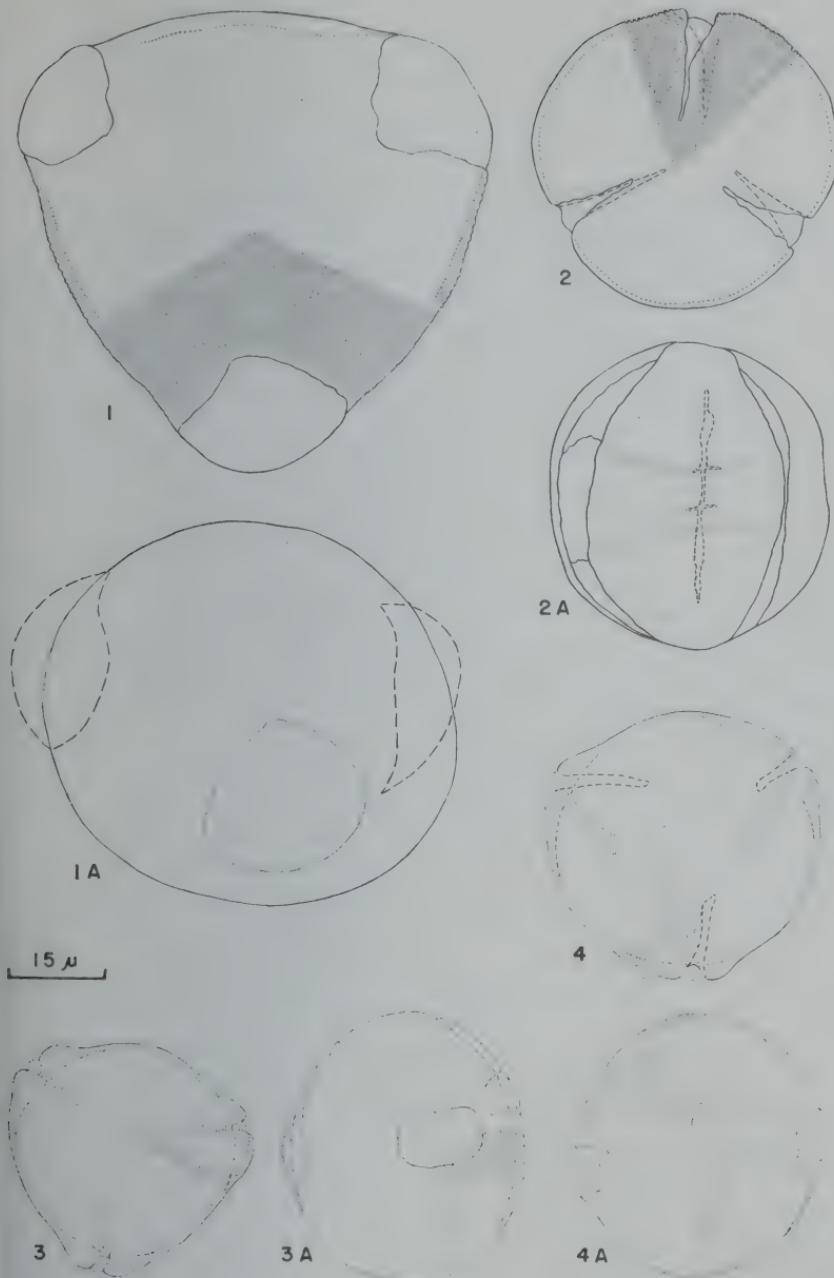
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DESCRIPTION OF PLATE I

The figures are based upon camera lucida drawings of unstained pollen mounted in lactic acid. The original drawings represent a magnification of ca. 1600-1700 \times . In the present publication the illustrations are reduced by approximately one-half.

FIG. 1. *Pseudobotrys cauliflora* (Brass 7005, A), polar view. FIG. 1A. ditto, equatorial view. FIG. 2. *Lophopyxis pentaptera* (collector unknown 1775, A), polar view. FIG. 2A. ditto, equatorial view. FIG. 3. *Metteniusa nucifera* (A. Jahn 1202, co-TYPE, NY), polar view. FIG. 3A. ditto, equatorial view. FIG. 4. *Metteniusa tessmanniana* (G. Tessmann probably 4042, TYPE, NY), polar view. FIG. 4A. ditto, equatorial view.



DAHL, POLLEN MORPHOLOGY

THE SEED AND GINKGO

ARTHUR J. EAMES

WHAT IS A SEED? When is a "seed" not a seed? For the seed — as for many other plant structures — no technical definition rigidly applicable is possible. The evolutionary history of this morphologically complex structure seems now fairly well known. The study of paleozoic reproductive structures of seed type has emphasized the fact that certain stages in the evolution of the seed cannot readily be set apart from others as "the seed." (Whether the seed arose through heterospory or through homospory is still in question and need not enter this discussion.) The various definitions and uses of the term seed cover every stage in the elaboration of the seed from fertilization to the presence of a mature, dormant embryo, and extend downward in the evolutionary series to cover the many types of paleozoic "seeds" which show no evidence of an embryo. In most botanical and popular definitions it is implied that a seed must have a dormant embryo. A frequently used basis of definition is expressed simply by Chadefaud (1944): "After fertilization the ovule becomes a seed." But in common usage for a long time, the fossil ovule-like reproductive structures of various taxa have been freely called seeds although they possess no embryos. Also, so-called seeds of *Ginkgo* and some cycads may have no embryo. Obviously, the term seed is loosely used. If it is to be used strictly, the line between ovule and seed must be drawn at fertilization. On this basis, it cannot be determined whether many fossil seed-like structures are ovules or seeds, and many complications of terminology, nomenclature, and classification arise. Nor can the plum-like "fruits" of *Ginkgo* that fall to the ground with the leaves be called with certainty, seeds or ovules; they may be either. In some conifers and some angiosperms, weeks, even months intervene between pollination and fertilization. What are the "ovules" to be called during the period when it is uncertain whether fertilization has occurred? Obviously, for convenience, the term seed must be used somewhat loosely, as are many other terms.

The use of the seed to characterize a natural group is now recognized as without value. The long-accepted "Spermatophyta" has disappeared from modern systems of classification because the possession of seeds brings together unrelated taxa, and the use of a group of other characters makes a more natural classification. Similarly, the "Gymnospermae" — characterized by the possession of *naked* seeds — also are now seen to be a highly unnatural group and the familiar and long useful term will soon be discarded in natural classifications.

It has been emphasized many times in recent years that natural relationships can safely be established only on groups of characters, not on a single character. Yet new classifications continue to be based on the seed.

Emberger (1942) has proposed the new group Praephanerogamae. On the basis that phanerogams differ from the Pteridophytes in the possession of an ovule (a megasporangium enclosed in tissues of the sporophyll), an intermediate group, the prephanerogams, stands apart as a taxon in which ovules are present but are shed without an embryo. The pteridosperms and cordaites form this group, as originally proposed. Favre-Duchartre (1945) added *Ginkgo* to the prephanerogams — rather illogically because, as he says, the falling ovules contain "des archégones encore vierges ou de jeunes embryons indifférenciées . . ." He calls *Ginkgo* the only living prephanerogam, yet describes it as having the distinguishing characters of both Emberger's prephanerogams and phanerogams. Emberger (1944), in his extensive textbook, maintains the Ginkgoales as phanerogams, stating that fertilization occurs only after ovules fall, though citing Favre-Duchartre. In his later description of the new group (1949), he includes both the Ginkgoales and the Cycadales "because of the published researches and observations of Favre-Duchartre (1943), Chadefaud (1944), Mangenot (1945), and Martens (1947)." "These [gymnosperms] are the last survivors of this group."

Florin (1950) has critically discussed Emberger's segregation of prephanerogams, and Martens (1951), in a review of the nature of the seed and its evolutionary history, has also discussed this new grouping of seed plants. Florin concludes that Emberger's classification "is artificial and should be rejected." This paper is written in support of Florin's view by emphasis on the importance of *Ginkgo* as a plant transitional between the prephanerogams and phanerogams of Emberger. It is written to bring attention also to the largely overlooked fact that *Ginkgo*, in its variations in time and place of fertilization, demonstrates an important step in the evolution of the seed — that of the transfer of fertilization from the ground to the mother sporophyte — and it adds information from the experience of the writer.

Unfortunately, details of the time and place of fertilization in *Ginkgo*, though known in a general way since the early studies of Strasburger (1872), have largely been overlooked or regarded as unimportant. But they are of much importance from the standpoint of such classifications as that of Emberger. Strasburger stated that fertilization may occur in ovules on the tree or after they have fallen, even "in a warm room," and that embryo development is the same wherever fertilization occurs. That fertilization may occur in ripe ovules on the ground as well as in unripe ovules on the tree has been largely disregarded, especially in this country. Van Tieghem (1884) states in his voluminous text that fertilization occurs in the ripe seed after its fall and that embryo development continues through the winter. Martens (1951) outlines the statements of various authors. Though Hirase (1894) at first described fertilization as on the tree, he later (1898) states that it occurs on the ground, though in some seeds on the tree. Ikeno (1901) states that fertilization occurs on the tree, that it may possibly occur on the ground, but that as far as he knows, "this has never been demonstrated." (Hirase also states that embryo

development may be completed on the tree or after falling. Apparently no other author has described full development of the embryo on the tree and Hirase's statement is probably in error.) Seward and Gowan (1900), in their memoir, apparently following Hirase, state that fertilization may occur before or after ovule fall. Strangely, neither Coulter and Chamberlain's textbook (1917) nor Chamberlain's much later text (1935) mentions place of fertilization. Chadefaud (1944) found that in Paris "ovules fall at the time of fertilization but also afterward." Studies made by the writer some years ago showed that in Ithaca, N. Y., fertilization may occur in late September in green ovules on the tree; in October in ripe ovules on the tree, or on the ground, even some days after they have fallen. The time of fertilization varied considerably in ovules on the same tree and among different trees in the same season and on the same tree in different seasons. Favre-Duchartre (1943) reported that fertilization may occur either just before, or after ovule fall, and that embryo development may continue to maturity even in the laboratory. Dangeard (1946) reported finding embryos in ovules on trees in mid-September in one year and in mid-August in another. Martens (1951) surmised that time of fertilization is climatically controlled. In the light of the writer's experience it seems more likely that it is related to age and time of pollination of the individual ovule. Fertilization in *Ginkgo* clearly may occur over a fairly long period and either on the tree or on the ground. The existence of this condition in a representative of a primitive seed-plant is important because it is probably an illustration of the ancient step in seed evolution when fertilization was transferred from the ground to the mother sporophyte. The survival of *Ginkgo* is, in one more way, most fortunate — as a demonstration of a critical step in the phylogenetic history of the seed.

Emberger's classification breaks down on the basis that *Ginkgo* falls in both of his groups. Further, Florin (1950) points out that Emberger's classification separates the Cordaitinae and Ginkgoinae from the Coniferae. And the growing opinion, substantiated by evidence from several fields, is that the Cordaitales, Ginkgoales, Coniferales, and Ephedrales form a natural group (Eames 1953).

DORMANCY IN PRIMITIVE SEEDS

Ginkgo, together with the cycads, illustrates another important step in the development of the seed, a step in the establishment of dormancy in the embryo. Though dormancy is often considered an essential character of the seed, the story of its development has received little attention. Dormancy of the embryo is an outstanding feature of the seeds of angiosperms and higher gymnosperms. The presence or absence of dormancy in the lower living gymnosperms — *Ginkgo* and the cycads — is rarely mentioned. In the lower fossil gymnosperms — pteridosperms and cordaites — the condition is unknown. Florin (1950) remarks "It appears probable that the ovules of the ancient gymnosperms always had a rest period, either after fertilization or after the shedding stage." He has also said

that the common absence of embryos in paleozoic seeds may well be explained "by the shedding of ovules rather than seeds." Arnold (1948) believes that paleozoic ovules were shed at a particular stage of maturity and that they entered a rest period at that time. (Arnold also suggests that the presence of a hard, durable integument enclosing the gametophyte may be evidence of dormancy in the ovules. But this condition is not necessarily evidence of a resting stage, for *Ginkgo* and some of the conifers, especially species of *Podocarpus*, have such histologically hard and tight layers before fertilization.) The writer agrees with Florin and Arnold that the ancient "seeds" without ovules are unfertilized ovules or seeds with early stages of embryos and that the absence of embryos suggests a resting period at the time of shedding or soon thereafter. Though *Ginkgo*, in its shedding of ovules and seeds with proembryos, shows in living plants the condition suggested for paleozoic plants, it does not give support to the existence of a rest period at this stage.

Neither *Ginkgo* nor the cycads show fixed dormancy at any stage; they do show induced dormancy, a dormancy induced by conditions unfavorable to continuous growth of the embryo or to germination if the embryo is mature. Such induced dormancy may well be a step to the fixed dormancy of other plants.

For *Ginkgo*, published statements imply embryo growth continuing until germination. Van Tieghem (1884) found embryo development through the winter. Hirase (1894) reports that the fall of the seed does not interrupt the growth of the embryo which continues until spring. Chamberlain (1935) states that embryo development continues in the laboratory or under stratification out-of-doors to germination in April; there is little or no dormancy, but development is more rapid in the laboratory. The writer followed embryo development in stratified seeds kept out-of-doors through the winter. (The seeds used were from a lot that had fallen and in which fertilization was occurring on the ground.) The studies showed that growth continued throughout the winter whenever temperatures were above freezing, and germination occurred in April without any apparent dormancy. Seeds held in warm places probably do complete embryonic growth and lie dormant until conditions are favorable for germination; here dormancy is induced.

In the cycads also, embryo growth is often stated or implied as continuing after the seed is shed but direct statements concerning dormancy are rare. Baird (1939) states that in *Macrozamia reidlei* growth continues in the seed for over 12 months without cessation before germination. The author has noted a similar condition in *Cycas circinalis*, with embryo development through several months. Chamberlain (1910), describing the embryogeny of *Dioon edule*, states that in this plant germination occurs without a dormant period but that seeds germinated after lying in a laboratory for over two years. Chamberlain later (1919) wrote "the cycad has no resting period, development being continuous from fertilization to old age and death."

Doubtless in both the cycads and *Ginkgo*, embryo development is con-

tinuous until germination under favorable climatic conditions, but dormancy may develop under conditions unfavorable to germination. Dormancy is not fixed but may be induced. These plants provide a step between continuous embryo-seedling development and the establishment of a dormant period at a determined stage in embryo development. In definition of the seed, no line can be drawn between the absence and the presence of dormancy in the embryo. It may be desirable — it is certainly convenient — to draw a line between the ovule and the seed, the presence of an embryo of any stage determining a seed. But it is a bit awkward to say that the *Ginkgo* tree sheds both ovules and seeds — that some of the fruit-like structures are ovules and others seeds without being able to point out which are which.

Summary. The definition of "seed" is discussed and the bearing of *Ginkgo* and its "seeds" on Emberger's segregation of Prephanerogams from Phanerogams. *Ginkgo*, in that fertilization takes place either on the tree or on the ground, falls in both of these groups, showing the classification to be artificial. This genus shows the important step, in the evolution of the seed, of the transfer of fertilization from the ground to the mother sporophyte. With the cycads it shows a step in the establishment of dormancy of the embryo in the seed.

The writer wishes to acknowledge his indebtedness to Florin and Martens on whose papers he has drawn freely in this discussion.

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SOME FACTORS IN POLLEN GERMINATION CALCIUM SALTS, DEXTROSE, DRYING

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IN HONOR OF IRVING W. BAILEY whose pioneer studies in cell structure, behavior and organization have been an inspiration, this paper is presented. It is a brief summary and discussion of experiments reported at the last three meetings of the A. I. B. S. but otherwise unpublished.

Pollen is notorious for the uncertainty of its behavior in germination and tube growth. Yet very little work has been done on the factors involved. A few studies have been made as part of more comprehensive programs. Bungenberg de Jong and Henneman (1934) in their work on cell models and neutral salts reported on pollen. Smith (1939) tested indole-3-acetic acid as a pollen germinant. Loo and Hwang (1944) included pollen in a series of papers on indole-3-acetic acid, manganese sulfate and colchicine as growth stimulants. Thomas, Gauch and Dugger, Jr. (1952) extended work on boron effects to include pollen, and O'Kelley (1954) used C-14 sugars to examine the rôle of carbohydrates in pollen growth. A brief summary of the literature has been made by Nitsch (1953) in his review of fruit growth.

In the present study of pollen physiology suggested by K. V. Thimann¹ in 1945, it soon became apparent that information on pollen germination requirements was incomplete. The essential tools of a reliable germinating technique and a growth medium were still lacking. To develop these it was necessary to determine the factors involved in pollen growth and their operation in terms of cell structure.

A preliminary survey of chemical stimulants and environmental factors was made in March to June, 1946-1949, on 28 species of the Texas Gulf Coast. None germinated satisfactorily in water, but, used separately or together, calcium salts and dextrose sometimes stimulated both germination and tube growth. Potassium, nitrogen, phosphorus, manganese and carbonate ions, indole-3-acetic acid, acetic acid and ammonia were ineffective although potassium as KOH or K_2CO_3 produced pronounced swelling of the intine wall.² Of the environmental factors the significant ones appeared to be humidity and age rather than temperature, light or acidity.

Intensive work on calcium and the related strontium and barium salts was done in Texas in the spring of 1950 and that of 1951. *Crinum* was the primary plant material. In 1953 a similar study of the effect of drying

¹ The author wishes to acknowledge Dr. Thimann's interest and kindness in suggesting pollen as plant material.

² In M/40-80 KOH or under mechanical pressure in weaker solutions of either KOH or K_2CO_3 swelling of the intine was followed by rupture of the extine wall and escape of the entire cell with the intine wall intact. Emerged cells were enormously enlarged with a thin wall.

was made on pollen of *Crinum*, *Nothoscordum* and *Hymenocallis*. Germination in dextrose and other sugar solutions was studied in Cambridge, Mass., June–September 1954, using pollen from a number of Irid, Amaryllid and Liliaceous genera.

Experimental technique was simple. Equipment consisted of a compound microscope with ocular micrometer, hollow-ground glass slides and covers for germinating chambers, a gold prospector's scale (accurate to 1 mg. \pm), C.P. chemicals, procelain-distilled water, pipettes graduated to 1/10 ml. and a 100 cc. cylinder. Pollen for each experiment was taken from a single flower or anther from which it was dusted onto single drops of the solutions. All chemicals were used in concentration series with one or more controls in water and dextrose or calcium. Stock solutions (M/5, M, 4M or saturated) were kept at 9° C \pm . Series were made by progressively diluting the stock one half: dilutions of one tenth were less satisfactory. To obtain progressive stages of drying, anthers from a single flower were exposed to room conditions over a period of days or weeks often with one or more held for comparison in a saturated atmosphere.

For all experiments % germination, tube length and elapsed time were recorded at the end of two or more hours. Tube growth might continue longer but most germination had occurred by the end of two hours and there was no discernible change in germination figures after four hours.

Results of the experiments may be summarized briefly.

Calcium (at. wt. 40).— Calcium salts were used alone and in combination with M/40 dextrose. Pollen for the 1950 tests showed no germination in water or in M/40 dextrose; 1951 material had 0–44% germination in water, 0–91% in M/40 dextrose.

All of the calcium salts tested — $\text{Ca}(\text{NO}_3)_2$, Ca Ac , CaCO_3 , $\text{Ca}(\text{H}_2\text{PO}_4)_2$ — were effective alone in aqueous solution. They initiated germination in pollen of *Crinum* with none in water, dextrose or other solutions tested; they increased the percentage for pollen with some germination in water; they stimulated tube growth at least in the early stages.

Pollen response was dependent upon the concentration of calcium (FIGS. 1 + 2). Dilute solutions only were effective in varying degrees over a broad range (M/20–M/40960 \pm). Effective ranges for the different salts were: $\text{Ca}(\text{NO}_3)_2$ M/20 to M/5120–40960, Ca Ac M/20 to M/2560–40960, CaCO_3 sat. to M/5120, $\text{Ca}(\text{H}_2\text{PO}_4)_2$ sat. to M/2,500,000–10,000,000.³ All ranges showed a well-defined optimum and often a single optimum concentration. Characteristic optima for the 1950–51 material usually included several concentrations in the M/20–M/2560 range with a single optimum between M/160 and M/640 [$\text{Ca}(\text{H}_2\text{PO}_4)_2$ sat.–M/650,000 usually with no single optimum concentration].

Optima and the dilute limit of the total range varied. They were

³ Concentrations of the almost insoluble calcium carbonate and calcium acid phosphate were calculated from the amount of salt dissolving in 50cc. distilled water in two weeks. Since degree of solubility varies with the amount of CO_2 present and other factors, figures for these salts must be considered approximate.

characteristically at more dilute concentrations for tube length than for % germination. They shifted to more dilute concentrations also for pollen with increasing germination in water.

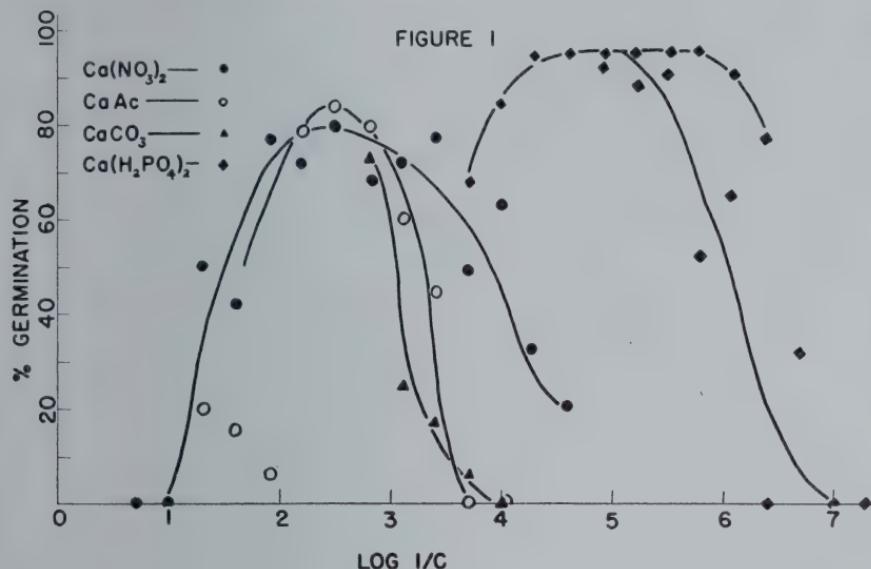


FIG. 1. Effect of calcium salts on % germination of pollen of *Crinum*; H₂O controls 0% except for the nitrate which was 18%, H₂O control.

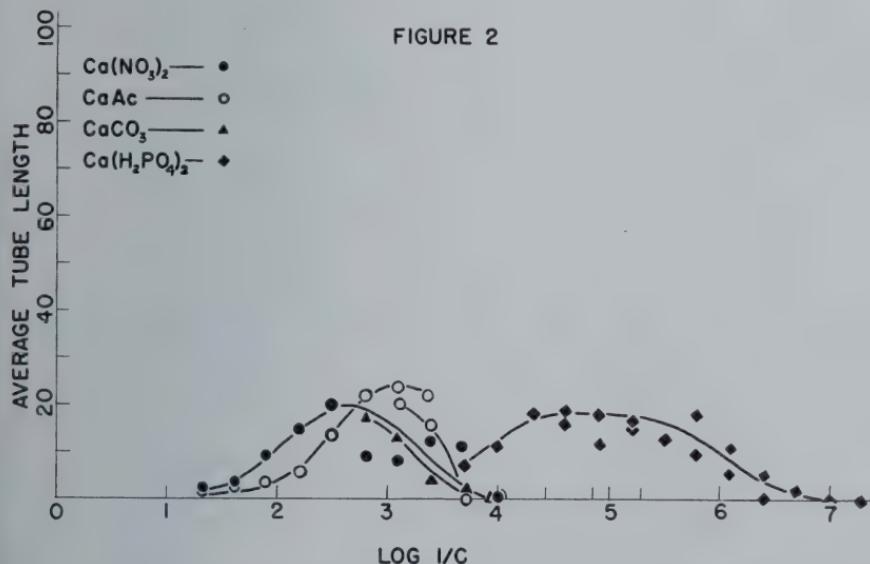


FIG. 2. Effect of calcium salts on tube length in first 2 hours of germination; water control 0. Curves for maximum tube length are similar but with values up to 50 and with a single optimum concentration for Ca(H₂PO₄)₂ as well as for the other three.

% germination and tube length were limited by extrusion of cell contents or by lack of response to a specific concentration of calcium. Early extrusion reduced % germination and tube length in the more concentrated portion of the range, and prevented tube formation in M/10 or stronger solutions. Lack of response seemed to be the limiting factor in more dilute solutions. Extrusion was not characteristic of this end of the range; the incidence of very short tubes declined while long tubes typical of the optimum persisted; very short tubes reappeared again in numbers only in the weakest concentrations of some experiments.

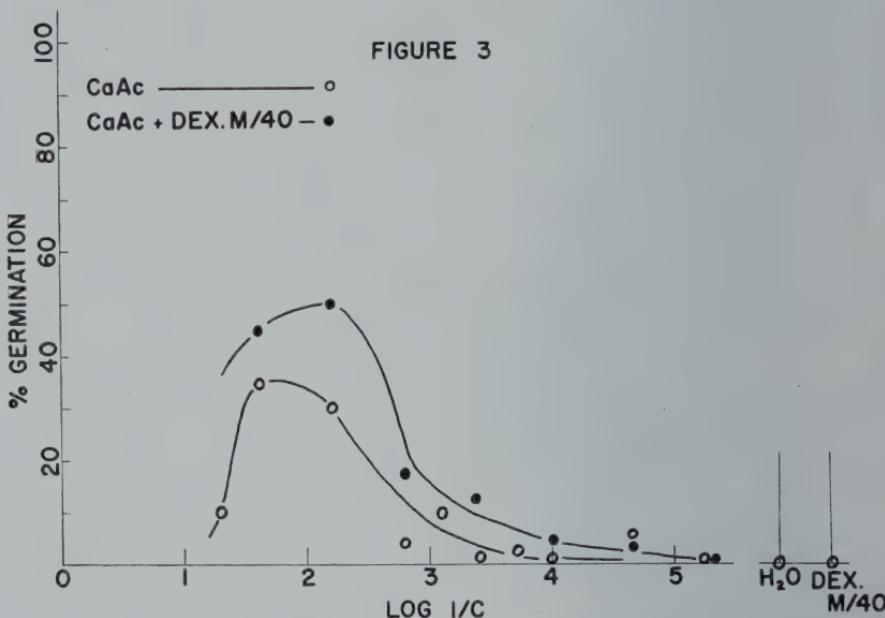


FIG. 3. Effect on % germination of adding M/40 dextrose to Ca Ac series. 1953 experiment; pollen of *Crinum*, stored 17 days.

$\text{Ca}(\text{NO}_3)_2$, Ca Ac and CaCO_3 were essentially alike in range, magnitude of effect and optima although CaCO_3 was soluble only in the more dilute portion of the range. $\text{Ca}(\text{H}_2\text{PO}_4)_2$ differed in that the total range extended to much greater dilutions while the optimum section was much broader with a recognizable single optimum concentration only in some of the data on maximum tube length.

Dextrose M/40 added to calcium solutions increased or decreased their effectiveness depending upon the condition of the pollen and the concentration of the calcium. For the 1950-51 pollen with low germination or none in water or dextrose controls, added dextrose increased % germination and tube length at most concentrations, extended the total range to greater dilutions, broadened the optimum range, eliminated the single optimum concentration or shifted it to a greater dilution, delayed or

prevented extrusion, gave more uniform tube length. The few instances of decreased germination and tube length occurred in strong or optimum concentrations and with pollen showing appreciable germination in water and/or dextrose alone.

Strontrium (at. wt. 87).—Two salts, $\text{Sr}(\text{NO}_3)_2$ and SrCO_3 , were tested alone and in combination with M/40 dextrose.

Both strontium salts resembled the corresponding calcium salts in their effect on pollen of *Crinum*, but were somewhat less effective. The strontium range, M/2560–5120 to M/40960+, was shorter, coinciding roughly with the dilute section of the calcium range and lacking the stronger solutions of that range. Effectiveness throughout the range declined rapidly as germination in water and/or dextrose reached zero: for increased germination and tube length, strontium was comparable with calcium only for two pollen samples with 7% germination in water and 1% in water, 15% in dextrose respectively. Tube length was often very short.

Response to added dextrose M/40 was marked, particularly where tube length and germination in strontium alone were low. It differed from that for calcium plus dextrose in that the strontium range was broadened at the concentrated as well as the dilute end and there was no shift of optima to greater dilutions. Decrease occurred only for tube length of pollen with germination in water (7%). It was appreciable and accompanied by a shift of the optimum to greater concentration.

Barium (at. wt. 137).— $\text{Ba}(\text{NO}_3)_2$ with and without M/40 dextrose was the single salt tested.

Pollen response to barium was even poorer than to strontium. In seven tests positive results were confined to one sample with the highest germination in water (15% vs. 0–8%). In this experiment the barium action, including the dextrose response, resembled that of the best strontium series except that the barium range was not extended by dextrose to stronger solutions.

Barium-dextrose solutions failed to produce germination in most solutions where barium alone was ineffective, but did produce germination and short tubes at low barium concentrations (M/20480+) in two barium negative samples with 6% germination in water and 0 in water, 4% in dextrose respectively.

Drying.—Material with high germination in water (50–95%) was secured for these experiments by using pollen from freshly opened anthers of the three plants selected,—*Crinum*, *Nothoscordum* and *Hymenocallis*. One characteristic of such pollen was the mixture of inhibition and stimulation that was shown in concentration series of calcium salts. Only the optimum solution or section of the range permitting germination showed any stimulation, and that often slight. All other solutions were inhibiting in various degrees (FIG. 4).

Pollen reaction to drying was marked by a decline in % germination accompanied by a change in the response to calcium and dextrose (FIG. 5).

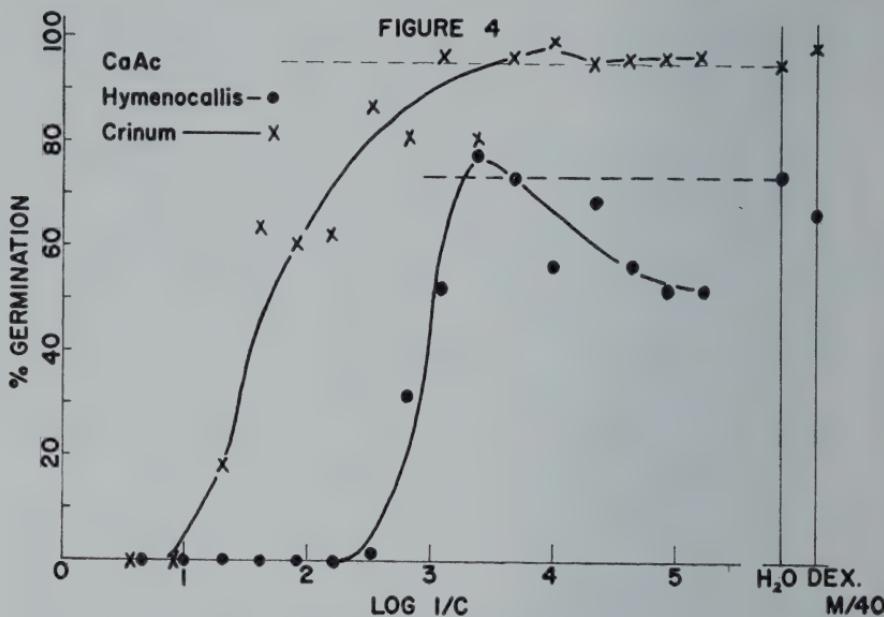


FIG. 4. Stimulation and inhibition by calcium in germination of fresh pollen with high germination in water; calcium acetate.

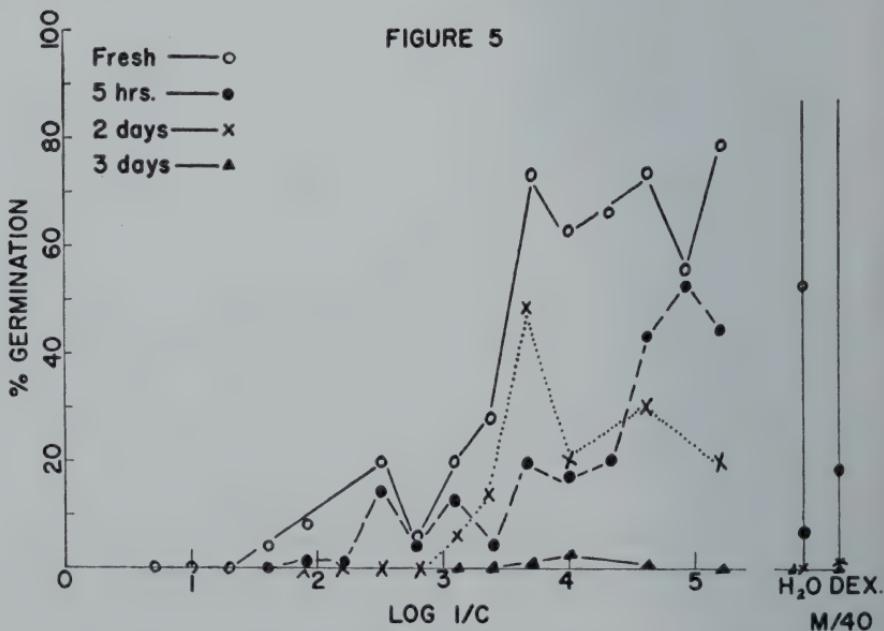


FIG. 5. Effect of drying on pollen response to Ca Ac; *Hymenocallis* pollen drying under room conditions.

These effects were counteracted or delayed by protection from drying either artificially or naturally.

Decline in germination was noted in all media. It was most rapid in water, more delayed and slower in calcium or dextrose. Water germination for pollen of *Crinum* and *Hymenocallis* commonly dropped to zero in the first 24 hours while optimum dextrose, calcium and dextrose-calcium solutions continued to show 50–90%. Germination in solutions containing calcium was retained longest; e.g. 3 days (Ca Ac) vs. 1 (H_2O) for *Hymenocallis* pollen, dry storage.

Decline in germination was retarded by storage under conditions reducing evaporation (FIG. 6). It was slower when pollen was stored in wax paper, in a moist atmosphere or at low temperatures; e.g. 5 vs. 2 day retention of water germination, moist vs. dry storage, *Crinum* pollen.

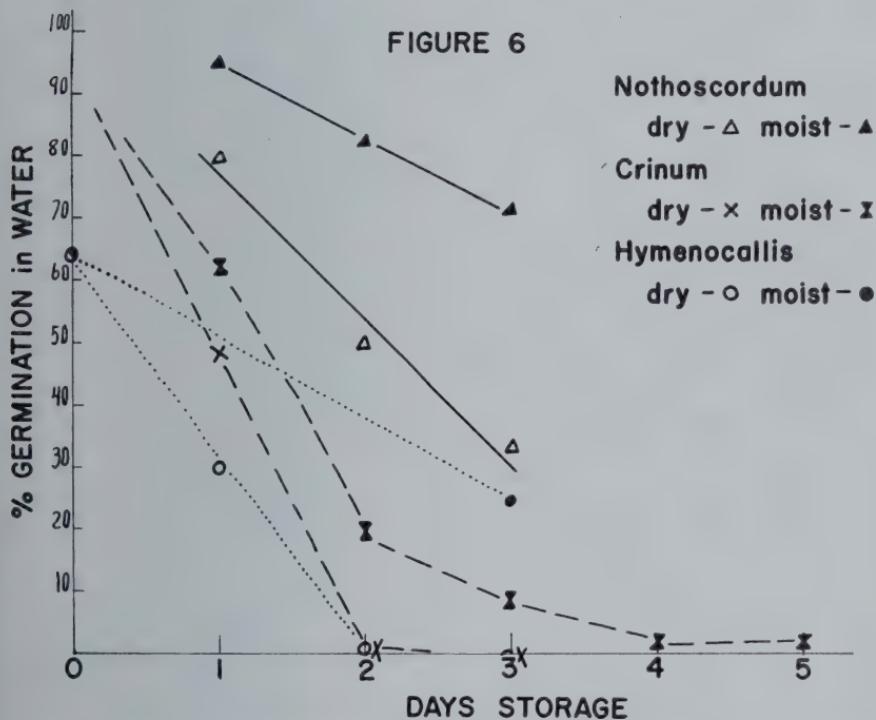


FIG. 6. % Germination in water of pollen stored in dry vs. moist air, room temperature.

Retention of germination varied with the species. With the Texas material, pollen of *Nothoscordum* showed germination longest (7 days vs. 1–2 for *Crinum* and *Hymenocallis*, water germination). Usually this species (*Nothoscordum*) did not show the sharp drop in germination in the first twenty-four hours characteristic of *Crinum* and *Hymenocallis* (water germination after one or more days often $80 \pm \%$ vs. 0–6% for *Hymenocallis*

and *Crinum*). In the Cambridge experiments in 1954, the two species with the longest retention of germination were *Narcissus* sp. and *Lilium regale* (up to 22 days, water germination, dry storage, and 40 days calcium-dextrose germination). Both species were characterized by very heavily massed pollen combined with copious tapetal material which, in *Narcissus*, hardened the pollen masses into cement-like pellets.

Calcium salts became increasingly effective as germinating agents in raising the % germination above that in water as pollen dried and germination in water dropped to zero (FIG. 7). At the same time an increas-

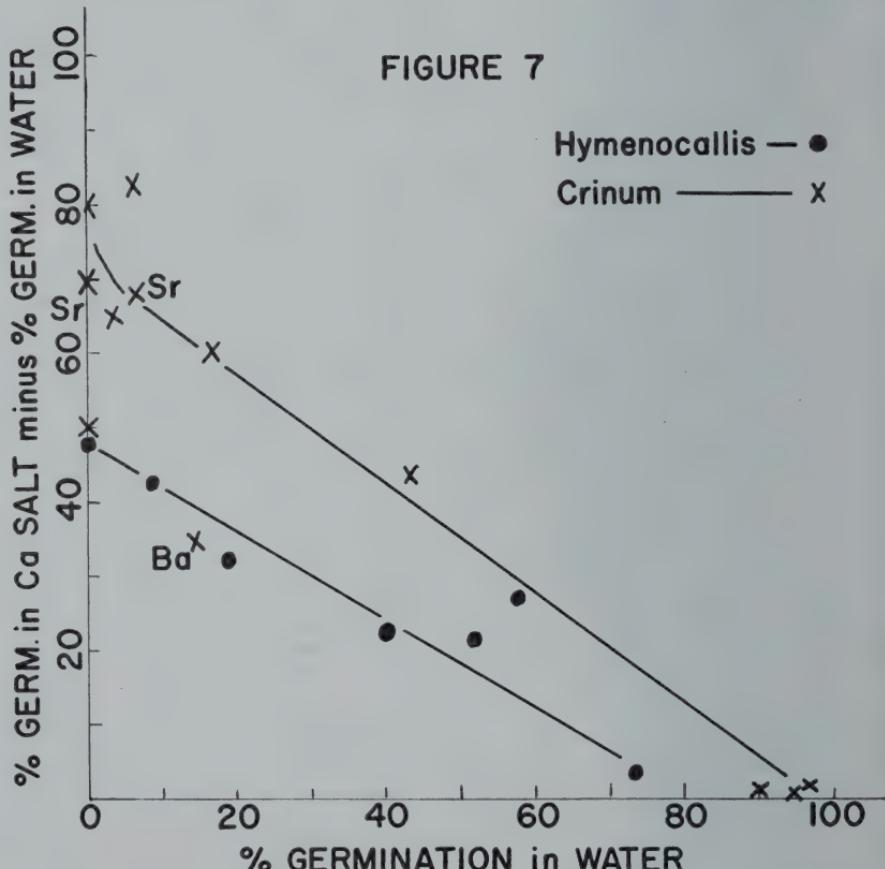


FIG. 7. Increase in effectiveness of calcium salts, Ca Ac and $\text{Ca}(\text{NO}_3)_2$, as germinating agents when pollen germination in water declines. Each figure is the optimum value for one of the longer series in 1951 and 1953 with pollen showing some germination in water or with pollen that has barely reached zero in water. A few figures for $\text{Ba}(\text{NO}_3)_2$ and $\text{Sr}(\text{NO}_3)_2$, are included.

ing number of partially or completely inhibiting concentrations became stimulating while optima and range limits shifted (FIG. 5). Optima shifted to greater concentrations as the range effective for stimulation be-

came broader until it included all concentrations permitting germination. Limits of the range in which germination occurred varied. Once established, the dilute limit shifted to stronger concentrations as drying continued. The concentrated limit was more erratic. With *Crinum* it usually remained at M/20 until the range began to shorten; with *Hymenocallis* it might shift from M/320 to M/80 first. Because of the continuous shifting the performance of a single concentration did not always follow the same course as that for the series as a whole and, particularly for originally inhibiting solutions, optimum germination might not be reached for one or more days (FIG. 8).

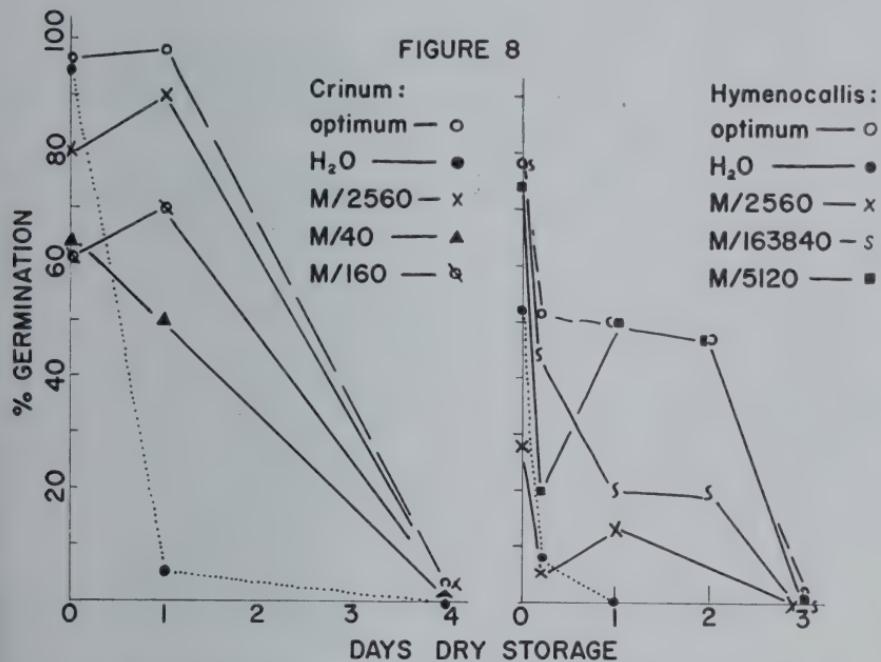


FIG. 8. % Germination of drying pollen in several concentrations of Ca Ac and in H₂O control. Pollen from one flower drying exposed to room conditions.

Observations on dextrose M/40-calcium combinations confirmed the findings of the 1950-51 experiments, but were somewhat inconclusive. To some extent the effect of added sugar was correlated with drying, but it usually seemed to be more directly dependent upon the effectiveness of the calcium. In any experiment where added dextrose M/40 increased germination in calcium solutions it was progressively more effective with concentrations showing lower percentage germination (FIG. 9); as pollen dried below <1% water germination, there was a tendency for the dextrose increase to be smaller in all but optimum concentrations. For *Crinum*, increased germination counteracted any calcium inhibition occurring in stronger solutions of the calcium range. For *Hymenocallis*, dextrose M/40

increases were confined to one series for pollen with 40% water germination and to single, weak, often barely effective dilutions (M/163840) in some other series. Added dextrose M/40 decreased germination in M/20–M/640 Ca Ac (optimum and stronger calcium concentrations) for pollen of *Crinum* with moderate germination in water (6–44%), and in M/40–M/163840± (practically the whole range) for most *Hymenocallis* pollen (0–75% water

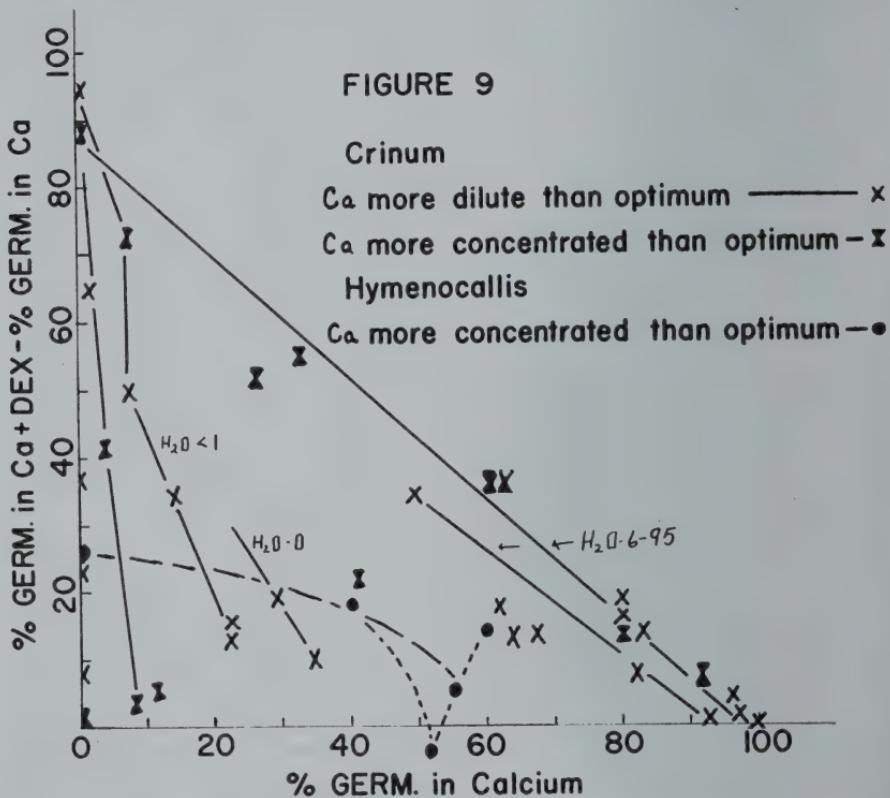


FIG. 9. Increased germination in Ca Ac with dextrose M/40 compared to % in same Ca Ac concentration alone. Lines connect data from one experiment; germination in water noted.

germination) (FIG. 10). With both plants the amount of decrease varied directly with the concentration of the calcium (FIG. 11).

Dextrose.—The most significant points shown by the dextrose series in 1954 were: (1) that dextrose like calcium was an effective germinating agent over a range of concentrations in varying degrees and subject to modification by the addition of calcium salts or by drying of the pollen (FIGS. 12 + 13); (2) that the dextrose range and effect differed from that of calcium in a number of details; (3) that dextrose under some conditions decreased or prevented germination.

The dextrose range lay mostly between M or M/2 and M/640, but it

sometimes included concentrations up to 4M (*Hymenocallis*) and dilutions to M/40960 (*Lilium regale*). Variations in range seemed to be correlated with the original condition of the pollen and the length of time that it was subsequently exposed to drying. The maximum concentration in ranges beginning at M or M/2 seemed to be fixed by pressure relationships, since pollen in stronger concentrations, with the exception of *Hymenocallis*, was unable to take up enough water to fill out the cells, and tubes in the first effective concentration were very short but intact.

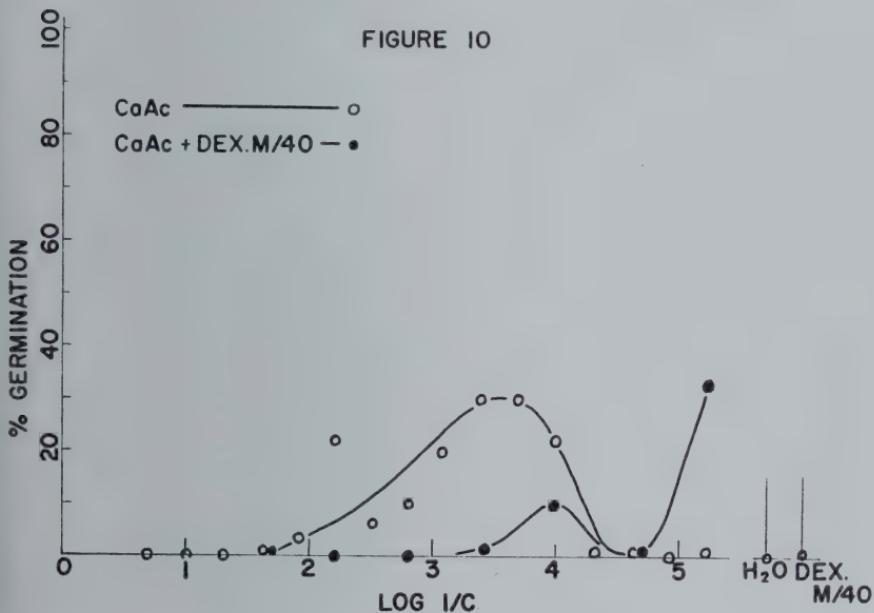


FIG. 10. Decrease in % germination of *Hymenocallis* pollen with dextrose M/40 added to calcium series.

The range for tube length at 2-4 hours was similar to but not identical with that for % germination.

The dextrose range differed from that for calcium in that it regularly included concentrations of M/10 and stronger and in that it customarily showed two well-defined optima and a very definite low. One optimum, usually the higher of the two, occurred in the more concentrated section of the range between M and M/20 (occasionally M and M/160). M/2, M/5 or M/10 were common values for this optimum. The second optimum was located in the dilute section of the range. It was more variable and occurred at a concentration between M/40 and M/320. The low which separated the two sections ordinarily was found to be M/20, M/40, M/80, occasionally M/10 or M/5 (*Crinum*). It was usually very pronounced, often an abrupt break, with germination sometimes reduced to zero or, for pollen with germination in water, to the point of partial or complete inhibition.

Drying affected germination in dextrose in some respects as it did that

in calcium solutions. As pollen dried, germination declined at a slower rate in dextrose than in water; appreciable germination continued in dextrose after it had disappeared in water; formerly inhibiting solutions of dextrose became stimulating. Optima, the low and range limits shifted. The range shortened, sometimes after an initial increase as in *Lilium longiflorum* ($M/10 \rightarrow M/2-M/80 \rightarrow M/5-M/20$), until germination was finally re-

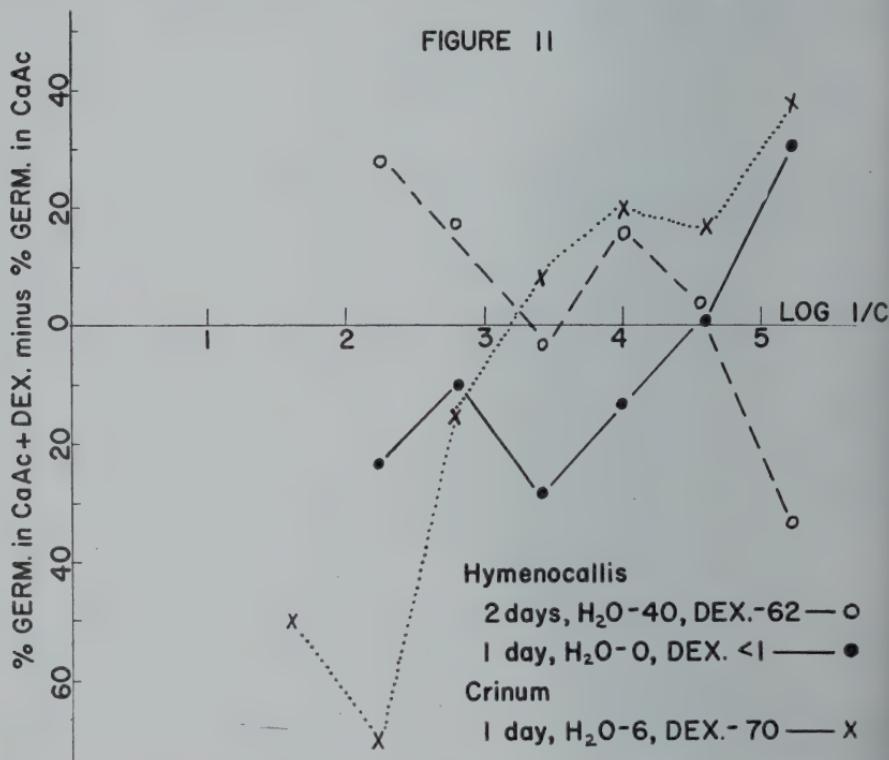


FIG. 11. Decreased germination in Ca Ac upon addition of dextrose M/40 correlated with concentration of Ca Ac.

duced often to two separated optima concentrations; germination in the stronger seemed to persist longest (*Crinum* M/10). Although both optima varied, the more concentrated one was relatively stable (*Crinum* M/2 for 4 days) while the dilute one shifted continually during drying. Selected concentrations, as in the calcium series, because of the shifting values, varied in performance so that one might show a marked increase or decline in contrast to that of the series as a whole and might reach its optimum value on the second or third day while the series as a whole continued a steady decline.

Unlike calcium, the decline in % germination in dextrose showed no apparently consistent relationship to % germination in water. It seemed to be more related to length of the drying period. Where there was suffi-

cient data on one species to be indicative, effectiveness of dextrose as a germinating agent seemed to decrease more or less irregularly with decreasing germination in water.

Calcium nitrate-dextrose mixtures showed: (1) that added calcium increased the effectiveness of dextrose series for pollen which through drying or otherwise showed lowered germination and shortened ranges in dextrose

FIGURE 12

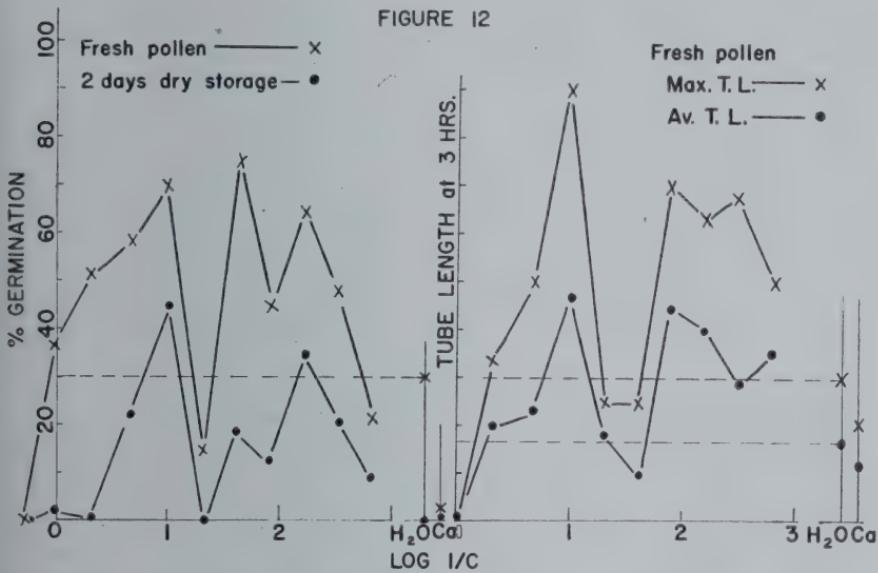


FIG. 12. Effect of dextrose on % germination and tube length of pollen of *Tulipa linifolia*.

alone; (2) that calcium concentrations ineffective in combination with dextrose M/40 were often effective combined with stronger dextrose (FIG. 13). Effectiveness varied with the concentration of calcium and of dextrose; it was modified by drying. In general a strong calcium solution (M/80) increased germination when combined with strong dextrose, decreased it when in dilute dextrose solutions; weaker calcium (M/320–M/1280) was effective throughout the dextrose range. With drying, M/80 calcium became effective in more dilute dextrose solutions while M/320, and even more M/1280, began to be ineffective.

Other Sugars.—Six other sugars have been given preliminary tests—sucrose, raffinose, levulose, galactose, arabinose and xylose. All, like dextrose but possibly in varying degrees, showed stimulation and inhibition of germination and a correlation between concentration and germination. However, pollen response in an equimolar test (M/10) including dextrose was not identical: three were positive, four negative. More tests were run on sucrose which was found to be more effective than dextrose at times; e.g. with *Iris* which did not respond to dextrose.

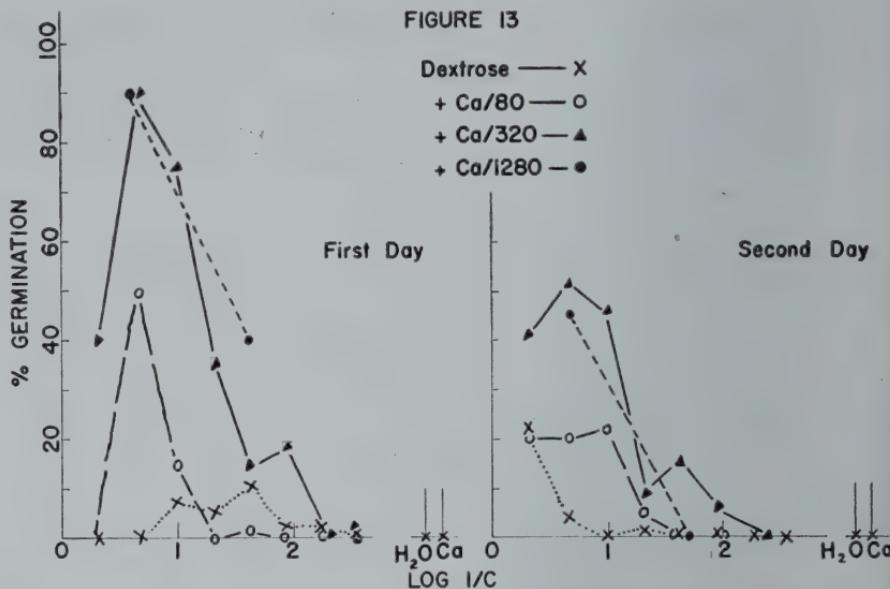


FIG. 13. Effect of Ca Ac added to dextrose series, *Hemerocallis* pollen.

DISCUSSION

It is evident from these experiments that there is at present no single technique or medium that will insure pollen germination although it may be possible to work out more or less widely applicable formulae. The 1953 experiments show clearly that drying or rate of water evaporation is an important factor in germination loss which with some species and under some conditions is very rapid. The 1950-51 and 1954 tests show that this loss of germination can be compensated for by the use of calcium salts or dextrose or calcium-dextrose mixtures, but that there is no one formula for all stages of drying. Germination in water can be used as a measure of drying which may be useful in securing or determining uniformity of pollen material for experimental work or in working out a formula for use with specific material.

The data on dextrose confirm the findings of others that $M/2-M/10$, $M/3$ concentrations of dextrose may be the most generally useful sugar concentrations since germination persists longer in sugar solutions just short of being dehydrating and reaches an optimum in this part of its range. It is more difficult to select concentrations of calcium since its effect seems to be even more dependent upon the degree of drying. For use with sugar, the stronger concentrations may include more, and certainly later, stages of drying but be inferior to more dilute solutions with less dried pollen. The failure of Bungenberg de Jong to obtain favorable results with a calcium-sugar formula was undoubtedly due to the use of too strong calcium with pollen showing high germination in sugar alone (95%).

To what extent other minerals are interchangeable with calcium has not been fully determined. Strontium and barium to a limited extent are; the order of their effectiveness is inversely that of their size or atomic weight — Ca, Sr and Ba. There is nothing in these experiments to contradict the findings of Loo, Gauch and others that boron (at. wt. 10) and manganese (at. wt. 54) in combination with sugar are effective pollen germinants. A comparison between Ca^{++} and the divalent Mn^{++} would suggest that Mn^{++} which chemically resembles Ca^{++} , might fall between calcium and strontium in effectiveness and, when used alone, be more limited than calcium in use with drying pollen.

The usefulness of indole-3-acetic acid has not been thoroughly explored. There is nothing in these experiments to suggest that it may not be a useful additive to dextrose as reported by Smith and others. On the other hand, if the interpretation of the dextrose experiments is correct, its chemical structure may indicate that its effectiveness alone is limited.

More significant than any practical application is the evidence presented of factors and mechanisms involved in pollen germination.⁴ Drying or rate of water evaporation is one factor operating before pollen reaches a germinating medium to reduce its ability to germinate. The presence of Ca^{++} , a mineral, and dextrose, a sugar, in the germinating medium are two other factors that can influence and control pollen germination.

That both pressure relationships and wall behavior are involved in the operation of these factors seems to be evident. Microscopic observation of pollen in strong dextrose (M/5 and stronger) indicates that stronger sugar solutions control germination through pressure relationships (osmotic, imbibitional or both) limiting the uptake of water by the pollen. The breaking of the dextrose range with the more concentrated portion showing relative stability during drying supports the conclusion that pressure control is a primary effect in this part of the dextrose range. Observation that stronger calcium concentrations (M/80), inhibiting alone or in more dilute dextrose, are effective combined with more concentrated sugar, tends to corroborate this view.

That the wall is involved in the action of calcium, dextrose and drying is indicated by practically all of the microscopic and experimental observations and is in accord with the conclusions reached by Thomas, Gauch et al for boron and its effect on pollen through cell wall and sugar transport. Stronger and inhibiting calcium solutions, intermediate inhibiting dextrose solutions limit germination by bursting apparently due to a weakened wall. Such solutions, the whole calcium range and the dilute section of the dextrose range are too weak to have any osmotic effects while neither they nor previous drying seem to affect the uptake of water by the pollen grain content. A comparison of pollen behavior in calcium and sugar solutions with that of cellulose or pectic-cellulose films indicates wall involvement; they show many points in common. The cellulose film (pectic) in pollen

⁴The author is indebted to J. Horace Faull, Jr., and Glenn A. Greathouse for their kindness in discussing some of the chemical theory involved.

is the wall. Both pollen and cellulose films take up Ca^{++} from dilute solutions; both pollen tube formation and elastic properties of a gel are affected by the sugar content; both % germination of pollen and water uptake of cellulose are decreased by previous drying.

That the intine rather than the extine wall is involved can be established by direct observation. The latter remains inert while the intine wall initiates tube formation and forms the wall of the developing tube.

A consideration of the known behavior of cellulose films and of the theoretical chemistry of high polymers (Meyer; Mark and Tobolsky) leads to the conclusion not only that the wall is involved, but that the calcium, dextrose and even drying act directly on the intermolecular structure which affects the properties of the wall and in particular its plasticity.

Hydration and dehydration are apparently of primary importance in determining the plasticity of cellulose for which water is one of the leading plasticizers. That water, aside from its rôle of creating pressure from within the pollen cell, plays an important part in germination is evident in the experiments on drying of pollen. In its general relation to rate of water evaporation, loss of germination through dehydration parallels the expected loss of plasticity in a cellulose film.

The rôle of calcium may be that of a hydrogen bond opener which breaks the H-bonding between linear cellulose groups to promote water uptake and plasticity. By forming calcium ionic bridges between cellulose members it may also increase the toughness of the wall. That both of these effects are involved seems likely. Tube formation depends upon both the plasticity of the wall and sufficient toughness to withstand internal pressure incident to its formation, although lack of toughness can be compensated for at least in part by reduction or counteraction of the pressure. Cf. pollen behavior in stronger concentrations of the dextrose range. Evidence supporting this view is found in the correlation between % germination of pollen and the concentration of Ca^{++} (calcium content is a determinant in the development of an elastic gel), and in the modification of the calcium concentration vs. % germination curve by drying of pollen. Since two properties are needed in proper balance, both directly dependent upon the Ca^{++} but one also involving subsequent hydration, they might be expected to develop at somewhat different rates with increasing Ca^{++} concentration. This would account for the irregularities in the $\text{Log } 1/C$ vs. % germ. curves beyond those due to experimental error. Excessive fluidity or stiffness, both inherent in the effects of increasing Ca^{++} concentration would limit the usefulness of the wall for tube formation and make it liable to the breaking under pressure characteristic of stronger calcium solutions.

The order of effectiveness of Sr^{++} and Ba^{++} and their greater restriction to pollen with specific hydration of the wall, if one may take % germination in water as a measure, is what would be expected from their size or atomic weights.

The apparent deviation of $\text{Ca}(\text{H}_2\text{PO}_4)_2$ in range limits and optima is not necessarily contradictory to the evidence in the similarity of the other three salts that calcium is the effective ion. The rôle of phosphorus in

sugar metabolism has long been recognized and it is known to be a degradent for cellulose. The phosphate ion might very well produce sugar within the cellulose wall which would have an effect on pollen similar to the addition of dextrose to the medium. Inspection of the $\text{Ca}(\text{H}_2\text{PO}_4)_2$ concentration vs. % germination curves and those of calcium-dextrose M/40 mixtures for comparable material shows a similar broadening of the optimum range, tendency to eliminate a single optimum concentration, extension of total range to greater dilutions and % germination increase beyond that of the Ca^{++} effect as defined by the other three salts alone for similar pollen.

The rôle of sugar beyond that of pressure control may be similar to that of calcium in increasing hydration and plasticity and in strengthening the wall. Inasmuch as interposition of the sugar molecule is through hydrogen bonding and not ionic bridges, its strengthening effect would be less than that of calcium. Because of its larger size, ability of the sugar molecule to penetrate drying cellulose is less even though its linear character may give better penetration than its molecular weight would indicate. The linear sugar structure may also provide additional slippage not found in the Ca^{++} , while its bulk opens more space for water.

Evidence is much the same as for calcium and emphasized by the similarities between the calcium and dextrose effects. The differences to be expected because of the somewhat different physical-chemistry of the sugar molecule and the Ca^{++} are to be found in the shortening of the dextrose range at the dilute end, in the differences in range detail such as optima and irregularities in this same section, and in the somewhat poorer performance of dextrose with drying pollen.

The outstanding difference between the calcium and dextrose ranges is the inclusion of concentrations stronger than M/20 and the break separating the range into a dilute and a strong section. Both may be attributed to the pressure effects of dextrose which seem to dominate the stronger section while evidence of wall conditioning is observable in the dilute section. The break occurs at intermediate concentrations where pressure control is declining and wall condition poor. Variation in location and magnitude of the break is a part of the variation in the dilute section of the range already discussed.

Dextrose inhibition like that of calcium, it may be worth noting, is easily explainable in terms of wall conditioning.

In calcium-dextrose mixtures the apparent dominance of the calcium, particularly with drier pollen, may be attributable to its better penetration of the cellulose lattice which might facilitate entry of the dextrose molecule. Otherwise the sometimes favorable, sometimes unfavorable response to the mixtures is what might be expected from the large number of not always compatible wall effects involved.

Tube length in the first hour or so, to the extent that it is a measure of germination, may be explainable in the same terms as pollen germination. But the problem of later development is a separate one already beginning

to appear in the early tubes as an inspection of the data on tube length shows.

In conclusion it may be noted that the universal presence of sugar and calcium in plants and the equally universal problem of drying make the possible application of the findings of this study to ecology, floral structure and plant distribution most intriguing.

SUMMARY

Experiments to show the effects on pollen germination of Ca^{++} , Sr^{++} , Ba^{++} , dextrose, other sugars and drying have been reviewed and discussed both with respect to any practical application of the findings and to the evidence they present of factors and mechanisms involved in pollen germination.

A possible mechanism in terms of wall conditioning through the control of hydration and plasticity by drying, Ca^{++} (mineral) and dextrose (sugar) is suggested.

CAMBRIDGE, MASS.

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COMPARATIVE MORPHOLOGY OF THE FOLIAR SCLEREIDS IN BORONELLA BAILL.

ADRIANCE S. FOSTER

With five plates

INTRODUCTION

THIS ARTICLE REPRESENTS the continuation of the writer's studies on the comparative morphology and ontogeny of foliar sclereids in the dicotyledons. It is now evident that from a topographical point of view, laminar sclereids may be classified into two main types, viz.: diffuse and terminal. The diffuse pattern is illustrated by *Trochodendron* (8), *Drimys*, *Belliolum*, *Bubbia* and *Zygogynum* (3), *Illicium* (4) and *Olea* (1), in which the sclereids occur as solitary or clustered idioblasts distributed in the mesophyll without consistent relation to the veinlets or veinlet-ends. In contrast, the sclereids of certain other genera, such as *Mouriria* (10, 18), *Coryphadenia* (19) and *Memecylon* (10, 25) are predominantly terminal, i.e., they lie in direct contact with the tracheary elements of the veinlet endings. Aside from their diagnostic value in systematic anatomy (1, 10, 18, 19, 21) these two patterns of sclereid distribution pose a problem of considerable morphogenetic interest. Ontogenetic studies have demonstrated that the terminal sclereids of certain species of *Mouriria* and *Memecylon* originate from initials which are located from the beginning at the terminations of the procambial network of the developing lamina (11, 20). Diffuse sclereids on the contrary arise from cells in the future palisade or spongy parenchyma — or from cells in both regions — and in general are unpredictable in their distribution and time of origin in the developing lamina (9, 12). Experimental studies on the physiological factors which condition the expression of the diffuse and terminal patterns of sclerenchymatous idioblasts are highly desirable but as far as the writer is aware, have never been attempted.

In an effort to extend our limited knowledge of the morphology and diagnostic value of terminal sclereids, the genus *Boronella* was selected for investigation. This genus of the Rutaceae consists of three or possibly four species of low shrubs endemic to New Caledonia (7, 16). The selection of *Boronella* was prompted by the discovery by Schulze (24) that in several species of *Boronia*, a genus presumably closely-allied to *Boronella* (5, 7), the leaves are characterized by branched sclerenchymatous idioblasts which almost invariably lie at the terminations of the veinlets. The writer not only confirmed the accuracy of Schulze's observations on *Boronia* but found that terminal sclereids are also a prominent aspect of leaf structure in *Boronella*. The present study, seriously handicapped by the lack of fresh or preserved leaf material, represents apparently the first anatomical

investigation which has been made on *Boronella*. It is hoped that it may shed some light on the structure and systematic relationships of an interesting New Caledonian endemic.

SYSTEMATICS OF BORONELLA

Baillon (5) based his original description of the genus *Boronella* upon the species *B. pancheri*. Since the time of Baillon, the following additional species have been proposed: *B. francii* Schltr. (23), *B. verticillata* Guill. ex Engler (14), *B. parvifolia* Baker f. (6) and *B. crassifolia* Guill. (15). In a paper devoted to the problems of synonymy which have arisen in the systematic treatment of *Boronella*, Guillaumin (14) concluded that *B. pancheri* Baill. and *B. francii* Schltr. are identical and that they are not distinguishable from Baker's *B. parvifolia*. Consequently, as presently conceived by Guillaumin (16), the genus now consists of three species, viz.: *B. pancheri*, *B. verticillata* and *B. crassifolia*. Leaf material of each of these species as well as samples of several collections of *B. francii* have been examined in the present investigation.

MATERIAL EXAMINED

The writer desires to record his thanks to the following individuals who contributed the herbarium material of *Boronella* used in the present study: Dr. Richard A. Howard, Director of the Arnold Arboretum and Dr. Clarence E. Kobuski, Curator of the Arnold Arboretum and the Gray Herbarium of Harvard University (AA and GH); Dr. A. C. Smith, of the U. S. National Herbarium (US); Dr. H. L. Mason, of the University of California (UC) and Dr. Jacques Leandri, of the Muséum National d'Histoire Naturelle of Paris (Paris). Special appreciation is also expressed to Dr. G. F. Papenfuss for his aid in forwarding the herbarium material from Paris and to Dr. Knowles A. Ryerson who sent the writer dried leaf specimens of *B. pancheri* which had been collected by H. S. McKee at Marais Kiki, Plaine des Lacs, New Caledonia (McKee 1107).

A complete list of the sources of the leaf specimens used in this study is as follows:

- B. CRASSIFOLIA Guillaumin. *Buchholz* 993a (UC, US, AA); *Franc* 2439 (AA); *Balansa*, Feb. 1872 (Paris).
- B. FRANCII Schltr. No. 247 "F.P." (AA); *Franc* 247A (AA); *Franc* 247 (AA); *Franc* 247 (US).
- B. PANCHERI Baill. *Bonati* 247 (UC); *Franc* Jan. 5, 1916 (US); *Prony* s.n. (AA); *Le Rab*, 1900-1910 (Paris); *Franc* 247 (GH).
- B. VERTICILLATA Guill. ex Engler. *Franc* 1618 (AA); *Franc* 1618P (AA); *Franc* 1618, sér. A (UC); *Franc* 3018 (UC); *Franc* 1618 (GH); *Balansa* 1061 (US); *Bernier*, Oct. 1900 (Paris).

TECHNIQUE

In order to secure satisfactory preparations of cleared laminae, it proved essential to modify the general procedure used by the writer in his studies of leaf venation (13). Even after a prolonged sojourn in dilute NaOH, the leaves of all species of *Boronella* studied were opaque and dark in color. The problem was solved by transferring the partially cleared leaves — after very thorough washing in distilled water — to a strong aqueous solution of chloral hydrate (250 gr. chloral hydrate in 100 cc. H₂O). Within a few days, the leaves became semi-transparent and were then ready to be washed in water, dehydrated in alcohol and stained in safranin.

The technique used in processing the herbarium leaf specimens so that useful serial paraffin sections could be obtained was devised by Dr. Francis V. Ranzoni whose assistance and skill is gratefully acknowledged. His method is as follows. The material is first aspirated in 70% alcohol, washed thoroughly for about an hour in hot tap water and then treated briefly (for about 15 min.) in 5% NaOH. The next step consists in placing the specimens in "Stockwell's Solution" (17, p. 85) for 48 hours or longer, which results in making the material lighter in color and somewhat transparent. Then, in order to insure smooth sectioning, the leaf material is placed in a 16% solution of hydrofluoric acid for 7–14 days; this treatment not only softens the tissues but results in complete elimination of discoloration. After treatment with acid, the material is very thoroughly washed in water and then brought into pure paraffin by the usual tertiary-butyl-alcohol technique. Serial transections of the laminae were cut at 10–12 microns in thickness and stained for about 24 hours in a 1% solution of safranin in 50% alcohol. The use of tannic acid-iron chloride, in conjunction with the safranin, yielded unsatisfactory preparations characterized by the overstaining of all lignified elements, in particular, the sclereids.

As in previous investigations, the writer is greatly indebted to Mr. Victor Duran for his skill in photographing the preparations used as illustrations in this paper.

GENERAL HISTOLOGY OF THE LAMINA

Before describing in detail the form and distribution of the foliar sclereids, it will be essential to outline the salient features of the histology of the lamina of *B. crassifolia*, *B. pantheri* and *B. verticillata* as revealed by a study of clearings and serial sections. It must be emphasized that the observations recorded below are based on a study of samples of a very few collections of leaves of these species and hence may not adequately depict the range of inter- and intraspecific variations which exist.

1. **Epidermis.** In all three species, the outer walls of the cells of the upper epidermis are very conspicuously thickened and, as shown in FIGS. 8–10, are more or less separated from one another along their outermost radial points of normal contact. Sections of one collection of *B.*

pancheri (Prony s.n., AA), however, showed a better preservation of the epidermal layer and a clearly stratified character of the thickened portions of the outer tangential walls. Stomata are restricted to the lower epidermis and as shown by FIG. 10, the guard cells are apparently extremely small in transectional view.

2. **Hypodermis.** A distinctive aspect of laminar histology is the presence of a well-defined hypodermis situated directly beneath the upper epidermis. In the two collections of *B. pancheri* examined and in *B. verticillata* (Franc 1618 UC), the hypodermis consistently is a single layer of tightly-joined cells (FIGS. 9 and 10) while in *B. crassifolia* (Buchholz 993a UC) the hypodermis consists of two (in certain areas apparently three) layers of cells separated from one another by small intercellular spaces (FIG. 8). It seems entirely possible that the two-layered character of the hypodermis in *B. crassifolia* may prove a reliable diagnostic character of this species. The true morphological nature of the foliar hypodermis of *Boronella*, i.e., whether a derivative of the protoderm and hence the inner part of a true multiple epidermis, or a tissue independently derived from the ground meristem, can only be solved by ontogenetic study of adequately fixed material. (Cf. Foster (12, p. 70-71) for a discussion of the concepts of hypodermis and multiple epidermis.)

3. **Mesophyll.** As might be anticipated, this delicate region of the lamina is more or less distorted in sections of herbarium leaves. Its general structure however is evident and a well-defined palisade tissue, varying in thickness in the three species, is rather sharply demarcated from the spongy parenchyma (FIGS. 8-10).

4. **Secretory Cavities.** The secretory cavities or internal "glands," so characteristic of leaves in the Rutaceae (7, 24), are well-developed in *Boronella* although interesting differences appear to exist between the three species with reference to the position of the cavities in the mesophyll. In both collections of *B. pancheri* examined, the palisade parenchyma is devoid of secretory cavities and these structures are only found scattered in the spongy parenchyma directly below the lower epidermis of the lamina. Secretory cavities in *B. crassifolia* and *B. verticillata*, in contrast, develop hypodermally in both the palisade and spongy parenchyma and appear to be relatively abundant (FIG. 8). Whether these differences are consistent however can only be fully demonstrated by a more comprehensive survey of a wide range of material.

5. **Venation patterns and vein structure.** As far as could be determined, the simple, emarginate, petiolate leaves of *Boronella* are characterized by their opposite or whorled phyllotaxis and by a unilacunar type of node. The small obovate or spatulate leaves of *B. pancheri* differ in the pattern of major venation from the much larger leaves of the other species because of the extension into the lamina, as branches of the single petiolar bundle, of a pair of strong lateral veins. This type of "palmate" venation contrasts with the more strictly pinnate arrangement of the main lateral veins in *B. crassifolia* and *B. verticillata*. In all three species, however, the major and minor veins are extensively anastomosed and form a con-

spicuous network with very numerous veinlet endings which commonly lie in direct contact with solitary or clustered branched sclereids (FIGS. 1, 2, 3, 4, 7).

Transsections of the lamina reveal that the bundles are collateral in structure, and that the midrib bundle and the major lateral veins are accompanied by more or less well-developed strands of fibers (FIGS. 8-9). In *B. pantheri*, the midrib bundle is completely ensheathed by fibers while in the other species the fibers constitute two separate strands of tissue, one located at the periphery of the phloem and the other adjacent to the protoxylem of the bundle. The small veins and veinlet ends, in contrast, are devoid of fibers.

DISTRIBUTION OF SCLEREIDS IN THE LAMINA

An intensive study of cleared laminae from the various collections of *Boronella* has revealed two rather distinct trends in the topography of the branched sclereids. In all leaf specimens of *B. crassifolia* and *B. verticillata* and in certain collections of *B. pantheri*, the sclereids are predominantly terminal in position at the veinlet endings and sclereids isolated from the vascular system are comparatively rare in occurrence. As seen at low magnification, the consistent development of sclereids at virtually all vein endings throughout the lamina of *B. crassifolia* presents a striking and definitive pattern (FIG. 1). An entirely similar condition is characteristic of the leaves of *B. verticillata* and in both of these species, veinlet endings devoid of one or more ramified sclereids, are extremely infrequent. At higher magnification, the form and abundance of sclereids associated with the veinlet terminations is plainly revealed. In both *B. crassifolia* and *B. verticillata* there is a conspicuous tendency for groups of 2-3 sclereids to develop at the majority of the veinlet endings although in many instances solitary sclereids occur (FIGS. 2, 3, 7). Because of the complex branching of the sclereids, it is often impossible to determine accurately the exact number of sclereids in a given terminal group, as is clearly demonstrated by FIGS. 2 and 3.

The direct contact between solitary or clustered sclereids and the terminal tracheary elements of the veinlet can usually be readily seen in cleared leaves but is very convincingly demonstrated in transsections of the lamina. FIGURE 8, for example, shows at relatively low magnification a large vertically oriented sclereid at the terminus of a short veinlet in the leaf of *B. crassifolia*. The intimate "ball and socket" relationship between a pair of large ramified sclereids and the tracheary cells of the veinlet end is exceptionally well-displayed in the transsection of the lamina of *B. verticillata* shown in FIG. 9. Because of the intricate pattern of the minor venation and the recurved orientation of a large proportion of the veinlet endings, transsections comparable to those shown in FIGS. 8 and 9 are infrequent but sufficient examples were studied to demonstrate the precise nature of the contact between sclereid and tracheid.

In striking contrast to the predominance of terminal sclereids in *B.*

crassifolia and *B. verticillata*, the topography of the foliar sclereids in *B. pancheri* and *B. francii* is highly variable. Remarkable fluctuations occur with reference to sclereid position, not only between leaves from different collections but even between the leaves of the same herbarium specimen. On the whole, the general trend is towards the development of diffuse sclereids, which occur as isolated or clustered idioblasts unrelated to the veinlets or veinlet ends (FIGS. 5 and 10). This is the condition in the leaves of the majority of the collections of *B. pancheri* and *B. francii* which were examined, although in nearly all cleared preparations it was possible to find occasional sclereids lying at the terminations of some of the veinlets. Two of the most interesting examples of topographic fluctuations are, however, particularly worthy of emphasis in this connection. A survey of ten leaves from one of the collections of *B. francii* (Franc 247 US) revealed comparatively few diffusely-arranged sclereids and the majority of them were strictly terminal in position. In size and form, the leaves of this specimen entirely agree with those of other collections of *B. pancheri* and *B. francii*. The most remarkable example of fluctuation encountered in *B. pancheri* was provided by the collection Bonati 247 (UC). In two leaves, the great majority of the sclereids were situated at the veinlet ends (FIG. 4) while in many other leaves of this same specimen, most of the sclereids are scattered in the mesophyll distal to the veinlets (FIGS. 5 and 10).

The conspicuous trend towards the development of diffuse sclereids in *B. pancheri* and *B. francii* seems to be correlated with the dilation of one or more of the terminal tracheids of the numerous "free" veinlet endings. In some collections, only occasional veinlets terminate in enlarged or lobed tracheid-like cells (FIG. 5). But in several of the other collections, especially *B. pancheri*, Franc Jan. 5, 1916 (US), most of the veinlet ends are more or less dilated or club-shaped, and consist of one or of many ovoid or irregular tracheids. As shown in FIG. 6, the diffuse sclereids may be sparsely distributed between the veinlets, but in other collections with dilated vein endings (e.g., *B. francii* No. 247 "F.P.", AA; *B. pancheri* Le Rab, 1900-1910, Paris), the sclereids are excessively abundant and closely packed within the mesophyll.

FORM AND STRUCTURE OF THE SCLEREIDS

The predominant type of foliar sclereid in *Boronella*, regardless of its topography, is a profusely ramified cell, the branches radiating in various planes from the main or central "body" (FIGS. 1-7). As seen in transections of the lamina, it is evident that the vertically-directed branches of the sclereid extend into both the palisade and spongy parenchyma tissue (FIGS. 8-10). No examples however were seen in which the tips of any of the branches were in contact with either layer of the epidermis. In general, the sclereids conform to the type of so-called "astroscleireids" of Tschirch (26) although in *B. crassifolia* (Buchholz 993a, all collections), some of the sclereids are decidedly elongate and fiber-like in form. As shown in

FIG. 3, such fusiform sclereids commonly lie at one side of a veinlet and, when situated marginally, are branched in a bizarre and distinctive manner.

The thickness of the secondary wall of the sclereids tends to fluctuate considerably. In all collections of *B. crassifolia* examined, the lumen is reduced to a narrow channel and pits are sparse and vestigial in character (FIGS. 3 and 8). The sclereids of *B. verticillata* and *B. pancheri*, on the contrary, exhibit a more conspicuous lumen and small scattered pits are evident under high magnification at various points in the "body" of the cell (FIGS. 9 and 10). The nature of the pitting at the point of contact between a terminal sclereid and the adjacent tracheid however could not be satisfactorily determined from transections of herbarium leaves.

In addition to the branched type of terminal or diffuse sclereid, small brachysclereids or "stone cells" were observed in some of the leaves of collections of *B. pancheri* and *B. francii*. These idioblasts are never abundant and in all cases are restricted to one or two widely isolated areas in the lamina. Commonly the brachysclereids occur in small dense clusters and may in addition accompany, for short distances, the slender veinlets. There is no evidence that such cells were produced in response to injury and their sporadic occurrence and limited distribution within the species of *Boronella* is indeed puzzling.

The only other type of specialized idioblast occasionally encountered in *B. pancheri* and *B. francii* was a small tracheid-like cell resembling in its form and helical thickenings the modified tracheids of the vein endings. Idioblasts of this character were not seen in the leaves of either *B. crassifolia* or *B. verticillata*.

SUMMARY AND DISCUSSION

One of the most interesting results of this study is the discovery of the remarkable degree of fluctuation in the distribution of strictly terminal sclereids in the leaves of *Boronella*. Two of the species, *B. crassifolia* and *B. verticillata*, closely agree in having the majority of the foliar sclereids at the veinlet endings (FIGS. 1, 2, 3, 7, 8, 9). In marked contrast, sclereid topography is extremely unstable in the leaves of *B. pancheri* and *B. francii*. The range in variation in these plants includes the predominantly diffuse pattern of sclereids characteristic of most of the collections (FIGS. 5 and 6) and the combination of both terminal and diffuse branched sclereids which occurs within the different leaves of the same collection (FIGS. 4-5). The marked trend towards the development of modified, club-shaped free veinlet ends (FIGS. 5 and 6) and the sporadic occurrence of small brachysclereids, represent additional aspects of foliar specialization in *B. pancheri* and *B. francii* which were not encountered in the two other species.

The systematic implications of the variations in sclereid position in *Boronella* represent problems which demand for their solution the comparison of a much wider range of material than has been possible in the present investigation. Future studies should include a careful examination of the flower because the writer has observed a profuse development of both

terminal and diffuse ramified sclereids as well as "stone cells" in the sepals and petals of two collections of *B. pancheri*. The structure and topography of sclereids in the flowers of the other species possibly might provide additional information of morphological and systematic value as Morley (18, 19) found in his studies of floral sclereids in *Mouriria* and *Coryphadenia*. The nature of the interspecific relationships between the entities which have been included in the present study however can only be clarified by comprehensive anatomical and ontogenetic studies on all parts of the plant. But at least from the standpoint of the structure and topography of the foliar sclereids, there appears to be no valid distinction between *B. pancheri* Baill. and *B. francii* Schltr. In accordance with the conclusions of Guillaumin (14) and Engler (7), *B. francii* should probably be regarded as conspecific with *B. pancheri*.

In conclusion, it must be emphasized that the systematic distribution of terminal foliar sclereids in the dicotyledons proves to be considerably more widespread than has been realized. Sclereids which are predominantly situated at the veinlet endings in the lamina occur in the Melastomaceae (10, 18, 19, 25) Hamamelidaceae (11, p. 511), Polygalaceae (11, p. 511), Capparidaceae (21, 22) and Rutaceae (24). Very recently the writer has discovered that the large profusely branched sclereids in the leaflets of *Hannoa klaineana* Pierre & Engler (Simaroubaceae) are predominantly terminal in position. Further morphological explorations combined with intensive ontogenetic study are clearly needed and the results may be expected to yield information of systematic and phylogenetic importance.

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EXPLANATION OF PLATES

PLATE I

FIG. 1. *Boronella crassifolia*. *Buchholz 993a*. Portion of cleared lamina showing terminal sclereids. $\times 17$. FIG. 2, the same, showing solitary and clustered terminal sclereids at all veinlet endings. $\times 85$.

PLATE II

FIG. 3. *Boronella crassifolia*. *Buchholz 993a*. Portion of marginal area of cleared lamina showing clustered terminal sclereids. Note large branched fusiform sclereids at top and near center of photomicrograph. $\times 85$. FIG. 4.

Boronella pancheri. Bonati 247. Portion of cleared leaf showing well-defined terminal sclereids. $\times 85$.

PLATE III

FIG. 5. *Boronella pancheri*. Bonati 247. Portion of cleared leaf from same collection represented in FIG. 4. Note prevailingly diffuse sclereids and the enlarged irregular tracheids of certain veinlet ends. $\times 85$. FIG. 6. *Boronella pancheri*. Franc, Jan. 6, 1916. Portion of cleared leaf showing modified and dilated veinlet endings. Note diffuse but sparsely-distributed sclereids. $\times 85$.

PLATE IV

FIG. 7. *Boronella verticillata*. Balansa 1061. Portion of cleared leaf illustrating solitary and clustered terminal sclereids. $\times 85$. FIG. 8. *Boronella crassifolia*. Buchholz 993a. Transection of lamina showing at the right of the large collateral bundle a branched sclereid in contact with a veinlet ending. Note also the two-layered adaxial hypodermis and the conspicuous "gland" beneath lower epidermis at left. $\times 124$.

PLATE V

FIG. 9. *Boronella verticillata*. Franc 3018. Transection of lamina showing contact between a pair of ramified sclereids and the tracheary elements of a short veinlet ending. Note single-layered adaxial hypodermis which is separated from epidermis as a result of processing the leaf for sectioning. $\times 218$. FIG. 10. *Boronella pancheri*. Bonati 247. Transection of lamina showing isolated branched sclereid lying free in mesophyll. Note single-layered adaxial hypodermis and the small size of the guard cells of the stomata in the lower epidermis. $\times 173$.

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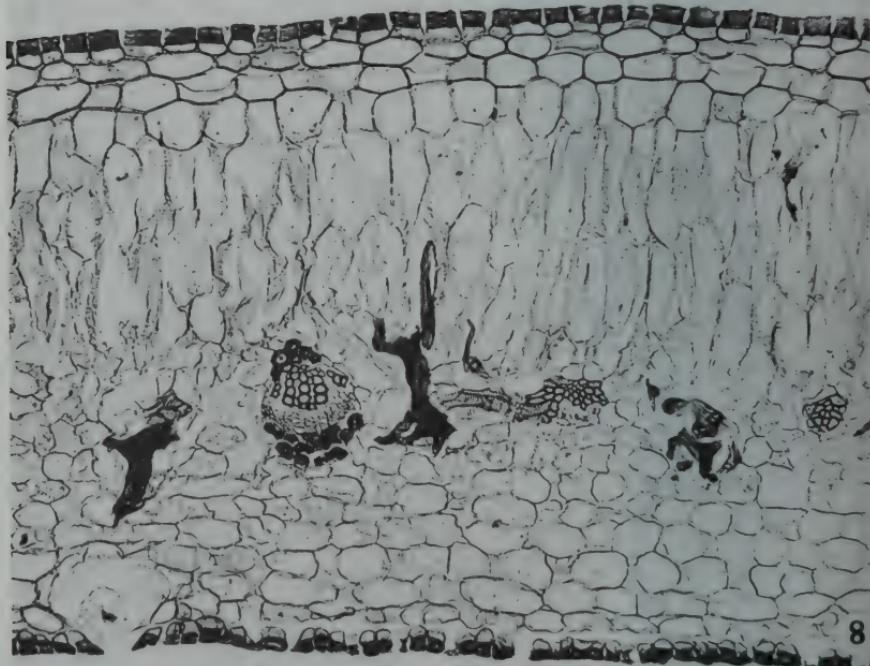
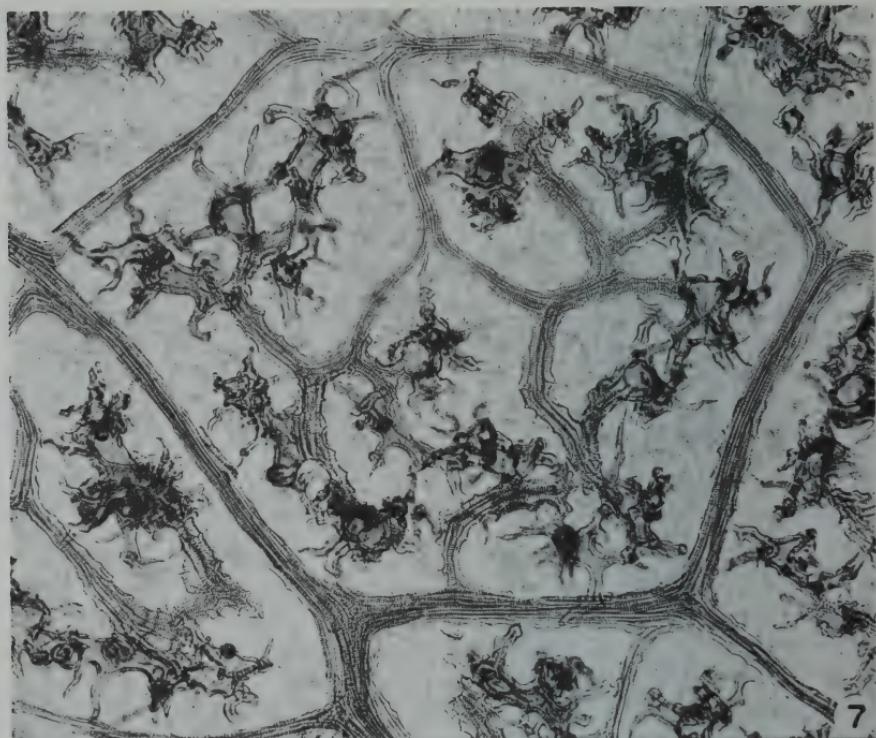
FOSTER, FOLIAR SCLEREIDS IN BORONELLA



FOSTER, FOLIAR SCLEREIDS IN BORONELLA



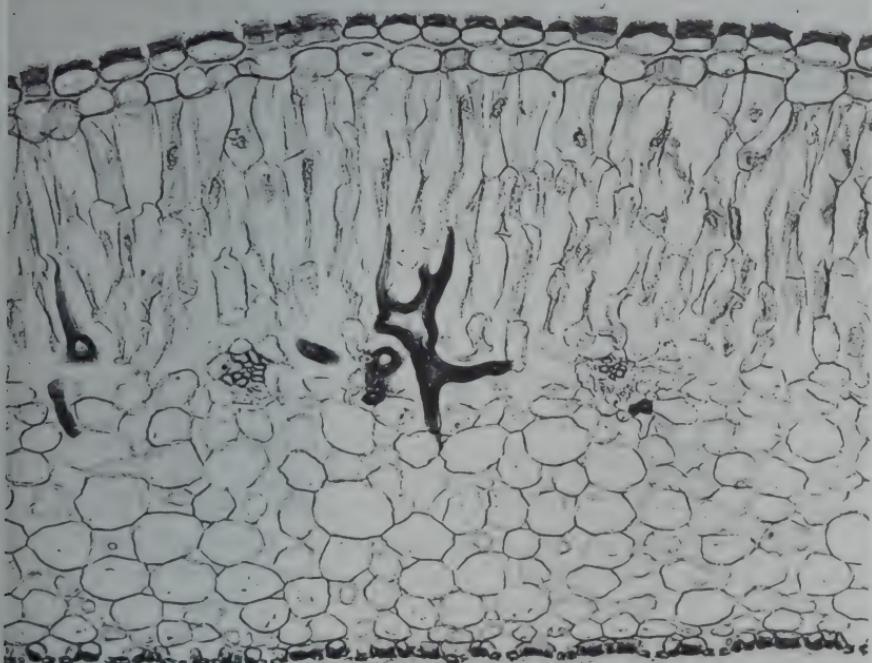
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FOSTER, FOLIAR SCLEREIDS IN BORONELLA

A TAXONOMIC REVISION OF PODOCARPUS
IX. THE SOUTH PACIFIC SPECIES OF SECTION
EUPODOCARPUS, SUBSECTION F

NETTA E. GRAY *

With one plate

SECTION *Eupodocarpus* as described in the first paper of this series (1) consisted of only four subsections; a fifth was added later (3) for an African species. Three species have subsequently appeared which, upon investigation of the leaf anatomy, require the addition of a new subsection (F) to the section. From New Caledonia, *Podocarpus longefoliolatus* had been described by Pilger (5) but the only specimen in the United States at that time, *White* 2037 in the Arnold Arboretum Herbarium, had not yet been identified as this species. *Podocarpus decumbens*, also from New Caledonia, was not collected until Chevalier and MacDaniels visited Montagne des Sources in 1949. *Podocarpus decipiens*, in the Fiji Islands, was found only after the examination of a large number of specimens determined by others to be either *P. nerifolius* or *P. elatus*. Differing from all other subsections of *Eupodocarpus*, the leaves have two or more resin canals above the vascular bundle (FIGS. 1-3). These are not closely associated with the transfusion tissue and in *Podocarpus decumbens* and *P. longefoliolatus* there are quite uniformly four. An additional pair of resin canals actually in the transfusion tissue is often found in *P. decipiens* (FIG. 4) as in subsection B (also South Pacific species in section *Eupodocarpus*) but these are considered to belong with those under the vascular bundle.

Although the two land areas of New Caledonia and Fiji are, geologically, both continental in type (4), they differ greatly in the number of genera and species of gymnosperms to be found in each. New Caledonia is very rich, with at least 37 species representing eleven genera. Few of the genera are monospecific and of the largest, *Araucaria* has had eight species described and *Podocarpus* twelve. In contrast, the Fiji Islands are poor in gymnosperms, having only nine species in four genera, *Podocarpus*, *Agathis*, *Dacrydium* and *Acmonyle*, all of which are also in New Caledonia. Again *Podocarpus* is the largest with five species. The three species of *Acmonyle*, a genus closely related to *Podocarpus*, are found only in New Caledonia and Fiji. In *Podocarpus*, five of the eight sections are found in New Caledonia but only three of these, *Dacrycarpus*, *Polypodiopsis* and *Eupodocarpus*, are also on the Fiji Islands. Of the species in section *Dacrycarpus*, *Podocarpus vieillardii* in New Caledonia is endemic, but *P. imbricatus* in the Fiji Islands is of wide distribution in the southwest Pacific, only not on

* The author wishes to express her great appreciation to Dr. Albert C. Smith, Curator in the United States National Herbarium, Smithsonian Institution, for kindly reading this manuscript and especially for his careful criticism of the Latin descriptions.

Australia nor New Caledonia. In section *Polypodiopsis* there are three species in New Caledonia, one species in northern South America, and one species in both Fiji and New Guinea. *Podocarpus vitiensis*, the latter, will probably appear on other Malaysian islands as more collecting is done. The Fiji Islands are the eastern limit of section *Eupodocarpus*.* In subsection B, to be described later, *Podocarpus sylvestris* and *P. novae-caledoniae* are endemic in New Caledonia and *P. affinis* endemic in Fiji. *Podocarpus nerifolius*, also in Fiji, has, on the contrary, what is probably the widest distribution of any species in the genus: from the mountains of Nepal east into China and the Philippines, into southeastern Asia and the vast area of the Malaysian islands, but not Australia nor New Caledonia. Subsection F is found only with the endemic species *Podocarpus longefoliolatus* and *P. decumbens* in New Caledonia and *P. decipiens* in Fiji.

The distribution of these species in New Caledonia and Fiji only is not common. Smith (7), in his studies of the Fijian flora, calculates that only 5.3% of the endemic species of phanerogams have their nearest relatives in New Caledonia or Australia. He names *Kermadecia* as an example of a genus known only from New Caledonia and with two species in the Fiji Islands. That *Podocarpus imbricatus* and *P. nerifolius* are absent in New Caledonia but otherwise widely distributed, and that the species of subsection F are distinct and endemic in New Caledonia and Fiji would substantiate Smith's assumption that "the last land connections to be sundered in this general region were those joining Fiji with the New Hebrides, the Solomons, and New Guinea" and "land connections between Fiji and New Caledonia were disturbed much earlier."

Podocarpus longefoliolatus, *P. decumbens* and *P. decipiens*, the species in this subsection, have two subulate bracts beneath the receptacle in the female cones and do not have the Florin ring in the subsidiary cells surrounding the stomata, characters which heretofore have been considered to distinguish subsection B from the others in *Eupodocarpus*. These characters are not common to all of the section *Eupodocarpus* in the land regions of the southwest Pacific, as the species assembled in subsection D, one of which is found in New Caledonia, one in Australia and Tasmania and the rest in New Zealand, do not have the bracts and do have the Florin ring.

Transverse sections of the leaves in subsection F show the single vascular bundle, hypodermal fibers, transfusion tissue and accessory transfusion tissue, upper palisade parenchyma and stomata only on the lower side which are characteristic of all members of *Eupodocarpus*. The lack of marginal resin canals and the Florin ring in the subsidiary cells surrounding the stomata are characters found only otherwise in subsection B of this section. Characteristics common to only some of the species in subsection B are auxiliary sclereids in the spongy and palisade parenchyma, fibers in the regions above and below the vascular bundle, interrupted hypoderm, and occasional fibers between the stomatal rows on the lower side. The two or more resin canals above the vascular bundle, distinguishing subsection

* Recent collections extend section *Eupodocarpus*, subsection F, into the Tonga Islands.

F from the others, were not noted by Orr (5) in his examination of *Podocarpus longefoliolatus*.

Podocarpus longefoliolatus Pilger in *Pflanzenreich* IV. 5(Heft 18):

79. 1903, in *Nat. Pflanzenfam.* ed. 2, 13: 248. 1926; Guillaumin in *Bull. Mus. Hist. Nat. Paris* 18: 100. 1912; Compton in *Jour. Linn. Soc. Bot.* 45: 426. 1922; White ex Wilson & Guillaumin in *Jour. Arnold Arb.* 7: 79. 1926; Florin in *Svenska Vet.-Akad. Handl. ser. 3, 10:* 279. 1931.

A small tree attaining 10–12 m. in height and 50 cm. in diameter; bark reddish and longitudinally furrowed, its outer layers sometimes grayish; branchlets thick with usually crowded leaves, the young stem ridged and furrowed from the base of the leaf petioles, the leaf scars round and flat on the older part of the twig. Terminal buds elongate with long-acuminate scales arising from a broad base, the outer ones spreading and becoming foliaceous and recurved, up to 10 mm. long. Leaves remaining on the twig for several years, coriaceous, patent to erect, straight or subfalcate, narrowly lanceolate, gradually narrowing at the base to a short, thick petiole, angustate toward the tip, acute to obtuse at the apex, sometimes shiny above, duller beneath, revolute at the margin when dry, 5–10.5 cm. long, 6–10.5 mm. wide; midrib broadly prominent or irregularly ridged above, scarcely distinct or only shallowly impressed below. Transverse sections of the leaves (FIG. 1) show interrupted hypoderm and 4 resin canals above the vascular bundle with three below. Pollen cones solitary, sessile, cylindric, 1.5 cm. long and 3 mm. wide, the scales narrowly triangular, the outer spreading, recurved and keeled. Microsporophyll tipped with short, thick, slightly incurved apiculus. Ovulate cones solitary in the axils of the leaves of the new growth; peduncle 1–2 mm. thick, angled, 1–1.7 cm. long; receptacle fleshy, about 8 mm. long, of 3 fleshy scales fused most of their length, free and spreading at the tips, subtended by 2 thin subulate bracts about 5 mm. long usually deciduous by maturity; bearing 1–3 (usually 2) ovules, bluish and glaucous when young. Seeds ovoid, 9 mm. long, 7 mm. wide, scarcely crested at the apex.

DISTRIBUTION: New Caledonia, found only certainly in rain forest on summit of Mt. Mou, 1000–1100 m. elevation, and perhaps on the nearby Isle des Pins.

SPECIMENS EXAMINED: *

NEW CALEDONIA: Mt. Mou, *Panchar s.n.* (type coll., P. 2 sheets, Herb. at Noumea), *Vieillard* 1265 (BM; P, 2 sheets), *Buchholz* 1098 († Ill), 1446 (A. † Ill), 1584 (Ill), 1682 (Ill), 1792 († Ill), *White* 2037 († A), *MacDaniels* 2324 († CU). LOCALITY UNCERTAIN: Isle de Pins, *Panchar* V1265 († ? P).

* The following symbols indicate the herbaria having the specimens cited: Arnold Arboretum (A), Bernice P. Bishop Museum in Honolulu (Bish), British Museum (BM), University of California at Berkeley (UC), Chicago Natural History Museum (Field Museum) (F), Cornell University (CU), Gray Herbarium (GH), University of Illinois Herbarium (Ill), New York Botanical Garden (NY), Paris Museum Herbarium (P), Stanford University Dudley Herbarium (DS).

† This symbol preceding the abbreviated name of an herbarium following the

This species was described by Pilger (6) from Pancher and Vieillard collections in the Paris Museum Herbarium which he found filed with *Podocarpus novae-caledoniae*. Foliage of *Podocarpus longefoliolatus* has been confused with *P. sylvestris* Buchholz, belonging to subsection B. The terminal buds of *Podocarpus sylvestris* are ovoid and differ in the thinner, closely appressed scales. Also *Podocarpus sylvestris* is found in different areas at altitudes below 500 m. The leaf transverse section shows only the three resin canals below the vascular bundle.

It is not certain if three specimens seen by Prof. Buchholz *in the Herbarium of New Caledonia at Noumea are this species (*Vieillard* 1275 from Bae du Sud, *Vieillard* 1275 from Wagep and *Vieillard* 1266 from Canala). Since these collections are not from the type locality of Mt. Mou where the only certain identification has been made, these must be excluded until further examination is possible. Pilger (6) listed the *Vieillard* 1266 from the Paris Museum but since Vieillard repeated his numbers for different collections the Noumea specimen must still be questioned. Compton did not collect *Podocarpus longefoliolatus* from Isle de Pins. A female specimen in the Paris Museum, *Pancher* V1265, is *Podocarpus longefoliolatus*, but the locality of Isle de Pins has been questioned.

The transverse sections of the leaves of this species show a thick cuticle and small vascular fibers are often abundant between the resin canals below the phloem but rare above the vascular bundle. The auxiliary sclereids present in the mesophyll are common in leaves more than one year old. Sometimes the palisade layer is more than one cell thick. The hypodermal fibers are usually in small groups on the upper surface of the leaf and are very rarely found between the stomatal rows on the lower surface. A 3-months-old leaf, from the specimen *Buchholz* 1446, gave some interesting light on the ontogeny of tissues and structures in leaves of *Podocarpus longefoliolatus*. The epidermis, transfusion tissue, and resin canals were fully mature. The xylem and phloem did not show complete cell wall thickening. The accessory transfusion tissue was remarkable in that it appeared so completely crushed that the cells could not be distinguished. Hypoderm and palisade parenchyma were not differentiated although many of the cells were already present. The mesophyll cells were large and were not crushed even though there was no apparent thickening of the cell walls. There were no vascular fibers.

Podocarpus decumbens sp. nov.

Frutex plerumque humilis 30–40 cm. altus, caudice primo 4–5 cm. diametro, ramis decumbentibus 2–3 cm. diametro interdum radicantibus, ramulis adscendentibus crassis glaucis, cum foliis confertis interdum

specimens examined signifies that the details of the leaves of this specimen have been examined in cross-section.

* From notes made by Prof. John T. Buchholz on his collecting expedition to New Caledonia 1947–48.

verticillatis, e basi petiolorum striatis et canaliculatis; alabastris ovatis, squamis longe acuminatis 6–10 mm. longis, vel exterioribus carinatis apice crassis et margine inferno erosionis, aliquando demum foliaceis ad 18 mm. longis, squamis interioribus triangularibus 3 mm. longis; foliis coriaceis, ex linearibus oblanceolatis, 3–5.8 cm. longis, 4–7 mm. latis, supra nitidis subtus glaucis apice obtusis, basi in petiolum brevem crassum angustatis; costa supra angusta et manifesta, subtus lata (at 1.5 mm.) et striata; foliis semper cum ductis resiniferis 3 sub vasi phloemate, 4 vel plus supra xylum; strobilis masculis ex alabastris sessilibus axillaribus, 1.5–2 mm. longis, squamis latis obtusis, cylindricis, 1.5–3 cm. longis, 3 mm. crassis, squamis demum late deltoideis, carinatis, scariosis et laciniosis, apice acutis; microsporophyllis 1.8 mm. longis, conferte imbricatis, apice crassis, fusco brunneis; strobilis foemineis et seminibus ignotis.

DISTRIBUTION: New Caledonia, only from Montagne des Sources, 900 m. alt., growing under forest among ferns and *Dracophyllum*.

SPECIMENS EXAMINED:

NEW CALEDONIA, Montagne des Sources, Chevalier in 1949 (TYPE + III), MacDaniels 2379 (+ CU).

The description of *Podocarpus decumbens* was written from the specimen collected by Luc Chevalier on Dec. 1, 1949, on his trip with Prof. L. H. MacDaniels who also collected a specimen which I have examined. The small male cones have fallen from the specimen but they are mature with open microsporangia and the basal scales are still on the twig where they were attached. The very low creeping habit is rare in this genus of trees but it is interesting to note that *Podocarpus gnidioides*, in subsection D, of similar habit and only a little larger, is also found on Montagne des Sources. There is no confusing these species in the field or herbarium as the foliage is very different, the leaves of *Podocarpus gnidioides* being only up to 2 cm. long and 2 mm. broad. Only the sketch made by M. Chevalier convinces me that the twig with such large leaves, up to 5.8 cm. long and 7 mm. wide, came from so small a mature plant.

Transverse sections of the leaf of *Podocarpus decumbens* (FIG. 2) show a small vascular bundle with lateral wings of transfusion tissue more than half as wide as the bundle. There are three resin canals below the vascular bundle, the two lateral often near the outer extensions of the transfusion tissue, variable in size. There are two to four resin canals above the vascular bundle, the outer two often located near the inner edge of the transfusion tissue and also variable in size. The accessory transfusion tissue sclereids have somewhat irregular shapes and larger intercellular spaces. The hypoderm is interrupted above (the fibers large) and is rarely doubled; and is absent below between the stomatal rows. Vascular fibers are abundant between the phloem and resin canals and rare above the vascular bundle. Auxiliary sclereids are abundant in the mesophyll. The palisade is of only one layer of cells and is interrupted by the occasional auxiliary sclereids. A single layer of cells similar in shape, though shorter, is arranged like palisade tissue on the lower side of the leaf. Epidermal cells

are one-third to one-half larger in *Podocarpus decumbens* than in *P. longefoliolatus*.

***Podocarpus decipiens* sp. nov.**

Arbor dioica ad 20 m. alta, plerumque minor raro fruticosa, cortice pallido, ramulis divaricatis; alabastri terminalis squamis crassis ovatis, exterioribus longe attenuatis, interioribus brevioribus apiculatis; foliis coriaceis levibus utrinque nitidis, subtus subfuscis, lineari-lanceolatis, interdum subfalcatis, fastigio supra costam plerumque complanato subtus suppresso, 6.3–13 cm. longis, 7–16 mm. latis, apice late acutis vel acuminate, basi in petiolum 6–12 mm. longum sensim angustatis; foliis semper cum ductis resiniferis 3 sub vasi phloemate, 2 vel plus supra xylum; strobilis masculis cylindricis subsessilibus axillaribus interdum fasciculatis, ad 5 mm. longis et crassis, squamulis numerosis valde carinatis basi circumdatis, saepe longe apiculatis (si pluribus in fasciculis propter ramulos intra basim); microsporophyllis apiculo longo angusto ornatis; strobilis foemineis axillaribus solitariis, pedunculo angulato 5–15 mm. longo enatis, maturitate puniceis; receptaculo squamis multibus coalescentibus 5 mm. longis composito, saepe 2-ovulato, bracteolis 2 membranaceis gracilibus 3–5 mm. longis basi subtento; semine glauco subgloboso, 10 mm. longo, 8 mm. lato, interdum obtuse cristato, inferne haud angustato.

DISTRIBUTION: In the Fiji Islands, on both Viti Levu and Vanua Levu, usually at altitudes over 700 m. on mountain slopes and summits.

SPECIMENS EXAMINED:

FIJI: Viti Levu: MBA: Mt. Ndelaiyoö, on the escarpment west of Nandarivatu, *Smith* 5075 (♂ and ♀) (TYPE + Ill) (A); 2 mi. down Mbä Trail from Nandarivatu on Malawathi Creek, *Gillespie* 4227 († Bish, UC); Mt. Koroyanitu, Mt. Evans range, *Smith* 4116 (A, + Ill); Mt. Nairosa, Mt. Evans range, *Smith* 4092 (A, + Ill); between Nggaliwana and Tumbeindreketi Creeks, east of Navai, *Smith* 6000 (A, + Ill), *Smith* 5992 (A, + Ill); vicinity of Nandarivatu, *Gillespie* 4034 († Bish, UC), *Gillespie* 4203 († Bish, + DS, UC); NAITASIRI: vicinity of Nasinu, 9 mi. from Suva, *Gillespie* 3444 († Bish, UC); REWA: Quarry beyond Lami village, *Gillespie* 4609 († Bish); Mt. Korombamba, *Parks* 20146 († Bish, UC); NAMOSI: *Parks* 20197 († Bish, UC). Vanua Levu: THAKAUNDROVE: Yanawai river region, Mt. Kasi, *Smith* 1769 († Bish, +F, GH, + NY, UC). Locality uncertain: Ra(?): *Degener* 15565 († A).

Podocarpus decipiens is usually a tree, often attaining sufficient size to be used in the lumber industry; it is called "asimbolo" throughout Viti Levu, but in the Mt. Evans region was noted as "ngali." On Vanua Levu it was recorded under the name of "mbau." It most frequently grows in dense forests on slopes and summits of mountains at altitudes over 700 m. where the angiosperm species, *Degeneria vitiensis*, was sought for and found much more abundantly than expected. However, *Gillespie* 4609 was found growing in limestone rocks only about 6 m. above a tidal swamp in Rewa Province, and *Gillespie* 3444 at 150 m. in southern Naitasiri Province. *Parks* 20197 is said to be from a shrub 1–2 m. high, suggesting

a possible habit similar to *Podocarpus decumbens* in New Caledonia, but since it is sterile and has leaves about four times the size of *P. decumbens* I prefer to include it as a juvenile specimen of *P. decipiens*. Gillespie did not indicate the shrubby or arboreal habit of his specimens. The outer terminal bud scales are usually long with attenuate, often foliaceous tips; *Gillespie* 4609 shows an extreme in its broadly ovate bud scales with long apiculate apices. *Degener* 15565, *Gillespie* 4609 and *Smith* 5075, 4116, and 4092 do not have leaves more than 10 mm. wide. The remaining specimens have broader leaves (*Smith* 6000 being the broadest with leaves up to 23 mm. wide) and usually come from the lower altitudes of the range. Most of the specimens have leaves with a broad, only slightly prominent midrib. This is in contrast to the abruptly prominent midrib in *Podocarpus nerifolius*. The margins of the leaves are not revolute.

Wasscher's recent interpretation of *Podocarpus nerifolius* has so much broadened the description that the usually thinner leaves (a most indefinite character) is the only external distinguishing feature. Both species grow in Fiji, but *Podocarpus decipiens* grows at higher altitudes and has the resin canals above the vascular bundle in a transverse section of the leaves. Hybridization between the two species no doubt occurs and this accounts for the difficulty in making a positive determination for some of the specimens.

Studies in the leaf anatomy of *Podocarpus decipiens* (FIG. 3) show an interrupted hypoderm of small fibers, 16–29 μ , similar to *P. nerifolius*. Occasionally a few lower hypodermal fibers have been found between the stomatal rows. The resin canals above the vascular bundle is a character distinguishing it from other species of *Podocarpus* found in the Fiji Islands. Below the vascular bundle there are three or five resin canals and above the bundle the number may vary from two to six. A total of as many as nine resin canals encircling the vascular bundle has been observed, and one pair may be found actually within the transfusion tissue (FIG. 4). In *Smith* 4092, 5992 and *Gillespie* 4227 no upper resin canals have been found. Auxiliary sclereids in the palisade and spongy mesophyll are sometimes quite abundant and at other times very rare and cannot be used as a distinguishing character. The transfusion tissue and accessory transfusion tissue are uniform and well-developed.

Smith 4116 is atypical in the early deciduous bracts below the receptacle in the young stage and the exceptionally long peduncle (9–25 mm.).

Although I did not have the opportunity to examine it, *Gibbs* 743, from Nandarivatu, at 900 m., is probably *Podocarpus decipiens* instead of *P. nerifolius* as suggested. The site of the collection (2) is the same as that of the type, *Smith* 5075 (8). *Gibbs* 819 (2), said to be from a "slender erect tree, general in the forest" at altitudes over 900 m., may also be this species. It definitely is not *Podocarpus elata* R. Br., as identified, for this species has not been found outside of Australia except in cultivation.

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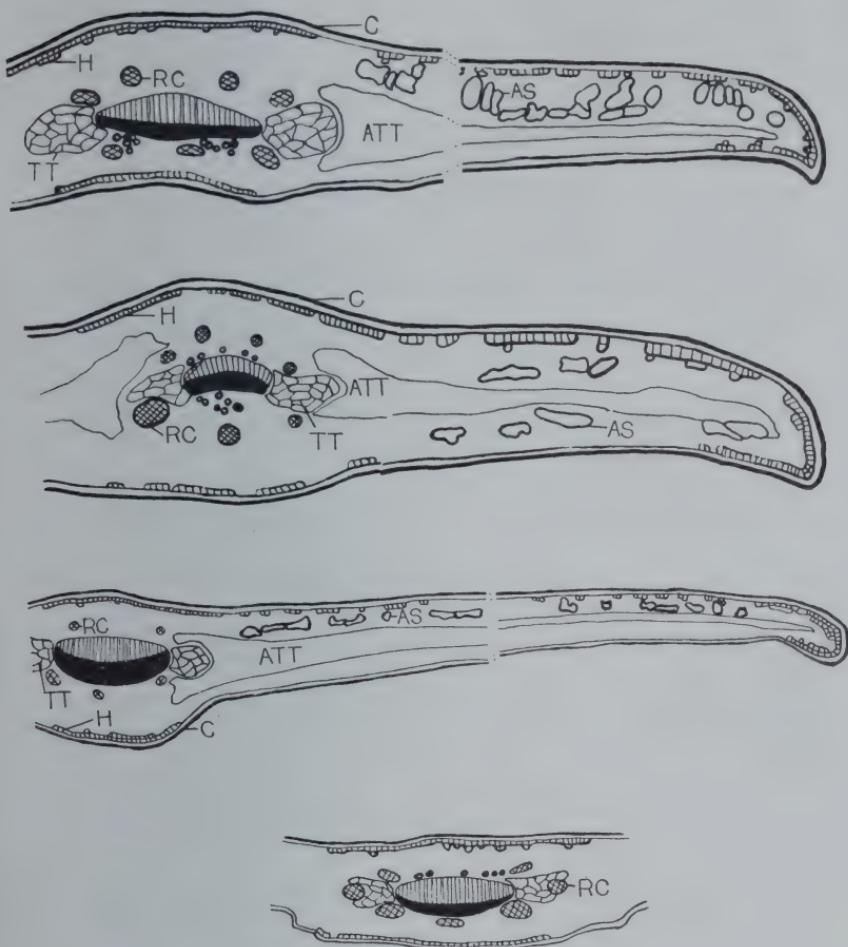
EXPLANATION OF PLATE I

FIGURE 1. *Podocarpus longefoliolatus* Pilger. Transverse section of leaf, *MacDaniels* 2324, showing relative thickness of (C) cuticle, extent of (H) hypodermal fibers, location of (RC) vascular resin canals with 4 above the vascular bundle, (TT) transfusion tissue, (ATT) accessory transfusion tissue, and (AS) auxiliary sclereids in the mesophyll. $\times 20$.

FIGURE 2. *Podocarpus decumbens* Gray. Transverse section of leaf, *MacDaniels* 2379, showing same tissues as FIG. 1, with 4 resin canals above the vascular bundle. $\times 20$.

FIGURE 3. *Podocarpus decipiens* Gray. Transverse section of leaf, *Degener* 15565, showing same tissues as FIG. 1, with only 2 resin canals above the vascular bundle. $\times 20$.

FIGURE 4. *Podocarpus decipiens* Gray. Transverse section of leaf, *Smith* 5075, showing only the tissues in the region of the vascular bundle, with resin canals in the transfusion tissue as well as 2 above and 3 below the vascular bundle. $\times 20$.



GRAY, PODOCARPUS

THE VEGETATION OF BEATA AND ALTA VELA ISLANDS,
HISPANIOLA

RICHARD A. HOWARD *

With five plates

PERHAPS THE LEAST EXPLORED AREA of the Greater Antilles is the southern promontory of the Dominican Republic, the province of Barahona. Only one unimproved road extends across this low-lying, triangular-shaped, dry waste of Eocene and Pleistocene limestone and through the thorn shrub forests and brush lands. Only the collections of Nash and Taylor, Ekman, and Howard are available from this area, and these represent scattered locations and incomplete records of a promising flora rich in dry-land and desert endemics. Off the southern tip of this promontory are two small islands, Beata and Alta Vela, which are the basis for this study. Beata and Alta Vela, geologically related to the tip of Barahona peninsula, are intriguing small bits of land in the Antilles. Both are important in the role they have played in the history of the Caribbean. Beata was visited casually twice by botanists, and until the occasion of my trip there, Alta Vela was unrepresented in the botanical records of the Antilles.

I had seen these two islands several times from the sea, land, and air. My desire to visit them was accentuated by the fact that Erik Ekman, perhaps the most thorough of botanical collectors who have visited Hispaniola, had never been on these islands. During his extensive stay in Haiti and the Dominican Republic Ekman visited many of the islands adjacent to this larger land mass. He published comprehensive studies of the vegetation on Los Siete Hermanos, Tortue, Gonave, and Navassa, and found on each richness of endemics and significant information on the relationships of the floristic entities in Hispaniola. Beata and Alta Vela, lying as they do, should contribute additional information in the phytogeographic puzzles of the southern peninsula of Haiti and the Barahona coastal ranges.

Thus, in planning a visit to the Dominican Republic in 1950, I wrote in advance to the government of the Dominican Republic for permission to visit Beata and Alta Vela. This was necessary because Beata is a naval station of the armed forces of the Dominican Republic, which also maintain on Alta Vela a lighthouse. My request was referred to Mr. Manuel de Moya, then Secretary of Agriculture, who took prompt action to grant my request and to expedite my visit to these islands. Instructions were given

* The botanical observations and the collections which form the basis for this paper were made in 1950 when I had the opportunity of spending seven months in the Caribbean Islands. This extensive trip was made possible financially by grants from the Penrose Fund of the American Philosophical Society and the Milton Fund of Harvard University. I am particularly grateful for this support.

to the commander of the destroyer escort vessel "27 de Febrero" to call at the Port of Barahona and to supply transportation as I wished. It is difficult to express adequately my gratitude to Mr. Moya and to the commander and men of this vessel for their complete cooperation in making this botanical expedition possible.

We left Barahona on August 7th, making the run to Beata in a few hours. This in itself stands in contrast to the visit Alexander Wetmore made to Beata in 1929, when he rented a sailboat and spent twenty-four hours getting from Barahona to Beata and three days on the return voyage. The crew of the "27 de Febrero" supplied transportation from the anchorage in the northwest corner of the island several times daily to shore and back to the boat. A cot was supplied me when I chose to sleep on deck rather than in the officers' quarters in the shorter bunk which had been offered below deck. The meals were those of the officers' mess and were rich with the natural products of the country and the sea and beaches of and around Beata. Plantains, cassava, and other root crops were supplemented and augmented with a great variety of sea food from the Caribbean, turtle steaks from animals we netted or caught on the beaches, and goats which the crew shot in the thorn scrub of Beata. Each day the ship lifted anchor and took me to a different section of the Beata shore line to explore inward, and a one-day trip was made to Alta Vela before the week I had allotted was up and it was necessary to return to Barahona. I enjoyed the hospitality and courtesy of the Dominican Navy and the company of the crew on many trips into the difficult vegetation of these islands.

Beata Island was apparently first seen by Columbus on his second voyage. On his third voyage, in 1498, Columbus is reported to have arrived at his former anchorage under the little island of Beata on the twentieth of August.

The first complete description of Beata appears in a report of the U. S. Coast Survey in Senate Executive Document No. 38 of the Fortieth Congress, 1868. This report considers both Beata and Alta Vela and mentions that "Beata island, the larger of the two, lies four miles south by east from Beata point, the southernmost extension of Barahona peninsula." The island is described as "five miles long and two miles broad mostly covered with brushwood from 50-80 feet high. The southern part is the most elevated and the northern end terminates in a long low point. Off the west point there is no bottom to 136 fathoms of line three quarters of a mile distant. The east side is very deep and the north and northeast sides connect to Beata point by a shallow white bank with the greatest depth being three fathoms."

Various reports of the richness and the utilization of Beata Island appear in the older literature and descriptions of the island, entirely unsupported by any evidence found on the island today. Moreau de Saint-Méry in 1796 described the abundance and quality of the wood on Beata, which indicated the high fertility of the land. Additional comment was made on the increase in the size of the herds on the island. Moreau felt it possible to establish estates with flocks of sheep, as existed in former times. James

Playfair in his *Geography* (6: 625. 1814) states, "On Beata the soil is good and was once in a state of cultivation. Till the fall of Santo Domingo, it was the great resort of French privateers." As recently as 1918 Otto Schoenrich (*Santo Domingo, A Country with a Future*, pages 113-114) described Beata as follows: "The island is covered with dense forests in which wild cattle abound. During the sixteenth and seventeenth centuries the island was a convenient resort for the pirates that infested the Spanish main; at one time it is said to have contained fine plantations, but at the present it is only occasionally visited by Dominican or Haitian fishermen." These reports are hard to believe in the light of a present-day examination of the island.

Only two modern visits to the island have been made by botanists, to the best of my knowledge, although zoologists and anthropologists have been there more frequently. The Danish Oceanographical Expedition with the steamer *Dana* explored the warmer parts of the Caribbean Sea and the Gulf of Panama in 1921 and 1922. Strong trade winds forced this ship to seek shelter on the west side of Beata on Feb. 22, 1922, and apparently it was anchored in essentially the same spot that Columbus chose. One of the botanists aboard this ship was C. H. Ostenfeld, who took advantage of the two-day lay-over to collect marine algae and to make a short visit ashore. The specimens of flowering plants which he collected were described by Urban in the *Dansk Botanisk Arkiv* 4(7): 1-37. 1924. Ostenfeld reports that they landed at the northwest corner of the island. "No inhabited human dwellings were to be seen but a grassy area mostly covered with *Panicum (maximum?)* and scattered cotton plants shew that formerly culture had existed here." Ostenfeld indicated throughout his brief report that the island was a difficult place to travel on or to collect plants.

Between 1929 and 1934 the expeditions sponsored by Allison Armour on his yacht the *Utowna* made several stops at Beata Island. I have been unable to date these specifically and have been able to locate only four records of plants collected during these visits. Thomas Barbour in his privately printed book, "Allison Armour and the *Utowna*," refers to his visits to Beata aboard the *Utowna* in the spring of 1929 and again in April of 1934. In 1932 the *Utowna* apparently made another visit to Beata Island, for one of the plants collected by the botanists aboard, David Fairchild and P. H. Dorsett, proved to be new and was described as a new genus *Armouria* (= *Ulbrichia*) of the Malvaceae. Mr. Harold Loomis, director of the Plant Introduction Station of the U. S. Department of Agriculture at Coconut Grove, Florida, was also on this expedition and introduced seeds of this new genus for cultivation in Florida. David Rogers, in his revision of *Stegnosperma* of the Phytolaccaceae, cites two other collections from Beata Island by these men. No collectors' lists or field books have been located for this expedition, although a gap of twelve numbers occurs between the *Stegnosperma* and *Armouria* collections.*

* After this paper was prepared I had the opportunity of visiting Mrs. David Fairchild at Coconut Grove and Mr. Harold Loomis at the Plant Introduction Station, also in Coconut Grove, Florida. Mrs. Fairchild kindly made Dr. David Fairchild's

Herbert W. Krieger, in an article on the Culture Sequences in Haiti (Smithsonian Institution Publication 3134: 113-124. 1932) refers to Beata Island and publishes a photograph of the shell mounds of pure *Strombus gigas* on the island. I was unable to determine the source of this photograph or the nature of the expedition. Alexander Wetmore visited Beata for a time in the spring of 1931, as he reports in the Smithsonian Institution Publication 3134: 45-54. 1932. He and his party hired a sail-boat and sailed for Barahona. Wetmore illustrated a small settlement called Ocrik on Beata Island and reported that his party stayed in one of the houses. The settlement at Ocrik was not in evidence during my visit in 1950. Wetmore's description of the vegetation indicated that it has changed little since Ostenfeld's visit, as he reports, "Thorny bushes, trees and vines growing from the scanty soil accumulated in crevices in the rock form a jungle so dense that it may be penetrated only along trails cut laboriously into the interior."

Thus I seem to be the first botanist to make a deliberate attempt to visit this island and to make comprehensive collections. I am not satisfied

field notes for this expedition available to me for study. She was also able to refer to photographs made on Beata Island, and her recollections of the Utowana's stay at Beata were most pleasant and helpful. Mr. Loomis, also, was able to refer to field books for information on his collections as a member of the party, and he had some excellent photographs of the area. From the field notes of Dr. Fairchild and Mr. Loomis I was able to prepare a numerical list of their collections on Beata, and Mr. E. C. Leonard of the U. S. National Herbarium has been most helpful in checking the herbarium for these specimens. He was not able to locate all of them, and in some cases in the following list field determinations are given. I am most indebted to Mrs. Fairchild, Mr. Loomis, and Mr. Leonard for their assistance.

The Utowana, with Fairchild, Dorsett and Loomis as botanists, stopped at Beata Island on January 17th and March 22nd, 1932. Only a single collection was made by Loomis on the latter date. He collected six numbers on the island on January 17th. Number 15 was identified in the field as *Coccothrinax ekmanii*. This is currently called *Haitiella ekmanii*. The specimen was not located in the National Herbarium. Numbers 16, 17, 18, 19 and 20 collected by Mr. Loomis were species of *Gossypium*. No material could be located at the National Herbarium. On March 22, 1932, Mr. Loomis collected a single number, 94, representing *Pseudophoenix saonae*. Mr. Loomis stated that Cook was in doubt regarding this identification at the time, but Mr. Leonard reports that a specimen so identified is in the National Herbarium.

The following collections by Fairchild and Dorsett were all made on Beata Island on January 17, 1932. Specimens present in the National Herbarium are indicated with an asterisk. All other names represent field identifications from Dr. Fairchild's field notebooks: 2603, *Guilandina ovalifolia*; 2604, *Opuntia moniliformis*; 2605, *Stegnosperma cubense**; 2606, *Stegnosperma cubense**. Number 2606 in Fairchild's field notebook is identified as *Zanthoxylum* sp. A specimen with the same number is cited by Rogers and is in the National Herbarium as *Stegnosperma cubense*. No. 2607, *Capparis flexuosa**; 2608, *Plumeria obtusa* var. *obtusa**; 2609, *Tribulus cistoides*; 2610, *Bromelia* sp.; 2611, *Exogonium eriospermum**; 2612, *Canavalia maritima**; 2613, *Maytenus reynosioides**; 2614, *Coccothrinax ekmanii*; 2615, *Rhynchosia minima**; 2616, *Indigofera suffruticosa**; 2617, *Ulbrichia beatensis*.

One addition can be made to the list of species from Beata Island given in this paper, on the basis of the Fairchild and Dorsett collections available in the National Herbarium. *Rhynchosia minima* (L.) DC. should be added to the Leguminosae.

that I have mastered the flora, however, and wish to pay a return visit at a different season.

Beata today appears from the sea to be a low flat island (FIG. 1). It is a large block of limestone which apparently has been tilted by coastal adjustments. The island is approximately five miles long and three miles broad, according to the skipper of the "27 de Febrero." It is shaped like a wedge of pie, broadest at the northern end and slightly rounded at the south. The north end (FIG. 3) is a sandy plain, at sea level, interrupted by shallow bays now filled with marine succulents and mangroves. The eastern side, likewise, is mostly level with the sea. The greatest elevation is approximately three hundred feet, at the southwest corner. The entire western side of the island shows a series of wave-cut benches with an escarpment of fifty to two hundred feet running from the coast at the north to a point well inland at the southern end of the island (FIG. 2). The surface of this major block is essentially flat, tilting slightly to the northeast. It appears, therefore, that this block of limestone has been tilted by sinkings on the northern and eastern edges. The first crustal adjustment was the most severe, but evidence of at least two other benches on the western side indicates subsequent changes in the attitude of the limestone.

Ostenfeld described Beata as "consisting of rocks of volcanic origin, being more or less horizontally lying light-colored lava-beds. There is often a short terrace of bare lava-rock; from it the inclination towards the water is nearly vertical, often interrupted by fissures and small caves into which the waves break with much noise." He made mention of the lush green vegetation on the coastal sand, accumulations of *Sesuvium portulacastrum*. Inland from the shore Ostenfeld noted that the most favorable place for the vegetation was in the lee of cliff faces. Above this was the flat but faintly sloping plateau. Ostenfeld climbed the cliff face and found on top a plateau covered with much wind-blown vegetation of low, many-branched trees. He comments, "Many lianas interweave the small trees and numerous cacti and other shrubs are scattered amongst the trees. It was very difficult to make a way through this vegetation, also because it was without any shade at all and extremely hot. The soil surface was nearly bare lava-rock which gave a sonorous sound when we walked on it, and loose soil was found in small holes and deepenings. It was really quite astonishing to find such a comparatively dense plant cover on this rocky surface." Further in his report Ostenfeld relates, "The difficulty in walking in this shade-less vegetation of 3-6 meters high trees, hindered by lianes and the stinging Cacti and other thorny shrubs, prevented me from proceeding far into it. At a distance some slender palms — *Thrinax* or another genus of the same appearance — rose above the low trees, but I could not reach into them. Therefore, I turned back, climbed down the steep cliff-wall to the shore-terrace and examined the vegetation sheltered by the wall." Ostenfeld concludes his report by stating, "Taken as a whole the vegetation shows that the climate must be very dry and probably the rainfall is very low, which together with the strong and constant wind produces the pronounced xeromorphism; but of course no meteorological

data are available. My visit was in winter which probably is the rainy season, but one did not get much impression of that, the only sign may be the shooting of new leaves on some of the *Bursera*-trees and the *Guaiacum*-shrubs."

I had the opportunity during my visit there to cover much more of the island than did Ostenfeld and to penetrate deeper into the spiny shrubland. I established as a starting point for most work the sandy beach area in the northwest corner of the island. This is the location that Ostenfeld mentioned where he saw a number of cotton plants, indicative to him of former cultivation. From this point I worked as far southward as possible on the western side of the island. I also penetrated directly eastward from that starting point and made a long trip around the northern end of the island, working due south from the north towards the interior, later continuing around the northern end and down the eastern side to a point beyond the abandoned salt ponds. Later, with the assistance of the destroyer escort, several landings were made along the west coast at favorable places, and penetration was made directly inland to the cliff face and onto the plateau in three locations.

Sea-level shore lines of Beata Island are of three types: sand, low limestone shelves or benches, and mangrove swamps. Small sandy beaches are common on the west coast (FIG. 2). One of these in the northwest corner of the island is now occupied by several buildings which form the on-shore headquarters of the naval units stationed at Beata. The sailors have attempted to grow some crop plants, but with little success, due to the low nutrients present in the sand and the lack of rainfall. With no accumulation of fresh water anywhere on the island, except in casual rock depressions, the buildings are used as catchments for rain water for the naval personnel. The largest sandy beach observed occurred on the northern end of the island, where on-shore winds have piled the sand on the outcrops of limestone rock.

The vegetation of the sandy beach areas is of the type found commonly in the Antilles (FIG. 2). *Panicum maximum*, an introduced grass, forms the largest stands of greatest height among the herbs. *Opuntia dillenii* occurs commonly at the edges of the grass. *Sesuvium portulacastrum* forms mats of succulent vegetation in open areas. Scattered and individual plants of *Tephrosia cinerea*, *Cenchrus pauciflorus*, *Cassia buchii*, *C. strigillosa*, *Corchorus hirsutus*, *Stachytarpheta jamaicensis*, *Indigofera suffruticosa*, and *Evolvulus alsinoides* occur on the open sand. Extensive development of the herbaceous vines *Ipomoea pes-caprae*, *Echites umbellata*, *Canavalia maritima*, *Passiflora suberosa*, and *Calonyction tuba* cross the open sand, and *Stegnosperma cubense* is rampant in protected areas near the stands of grass. To the rear of the open sand beaches, and especially in more sheltered areas, *Suriana maritima*, *Colubrina ferruginea*, *Lantana reticulata*, *Capparis flexuosa*, *Amyris elemifera*, *Jacquinia barbasco*, *Canella alba*, and *Caesalpinia anacantha* occur.

The limestone shelves are badly eroded and the surface is described as dogtooth limestone. Near the ocean the vegetation on these coastal shelves

is affected by the salt spray, about as described by Ostenfeld. In general all plants on these shelves are stunted and contorted. *Avicennia nitida*, *Amyris elemifera*, *Conocarpus erecta*, *Ernodea littoralis*, and *Rhacoma crossoptetalum* are the most common woody plants. *Cyperus nanus*, *C. planifolius*, and *Lithophila muscoides* are the most common herbaceous plants on the limestone benches. Further inland on the limestone benches the effects of the salt spray and the wind are less evident, and the vegetation becomes more luxuriant, approaching in composition that of the plateau area. Evidence of repeated tilting of the island can be found on the western side, where several small cliff faces exist before the main break to the plateau is found. Each cliff face shows undercutting due to previous wave action. These small caves are devoid of vegetation and are extremely dry. It is these caves that seem to be the habitat of the rhinoceros iguana (*Cyclura cornuta*) near the sea.

At the northern end of the island the transition from sand to limestone is gradual and migratory due to the wind action of blowing sand from the beaches onto the gently sloping rock (FIG. 3). The typical succulent beach vegetation gives way to extensive stands of grass and sedge and finally to a belt of pure sedge growth at the edge of the limestone. One of the conspicuous areas of the sedge belt near the limestone was composed of a large stand of *Remirea maritima*. The white bracts of this plant attracted the eye from a considerable distance.

The outcrop of limestone rock at the northern end of the island, exposed as it is to strong winds and salt spray, was occupied by an open stand of shrubby plants (FIG. 4). The rock in this region was heavily creviced and broken. Many of the plants found there were rooted deep down in the cracks with only the crown of the plant protruding. The few plants which did root in the small soil pockets on the limestone were strongly wind-blown, often with branches developing only on the leeward side of the plant. A few species, *Clerodendron spinosum*, *Erithalis vaccinifolia*, *Antirrhoea elliptica*, *Strumpfia maritima*, *Borrichia arborescens*, were found in this area alone on the island. The concentration of the palm *Haitiella ekmanii* in this wind-blown shrub zone was also unusual. *Haitiella* was found commonly in the interior of the island on the limestone plateau, but as scattered or individual plants. In the northern shrub zone just mentioned, however, plants of *Haitiella* were clustered (FIG. 4).

The third coastal type of vegetation, the mangrove swamp formation, was also most common on the northern end of the island. The shallow coastal waters and the gradually ascending beach area have combined to produce the type of shore line best suited to mangrove development. Apparently the profile of the shore line has varied in the past, due to shifting currents and deposition and removal of soil. Some of the mangrove formation is now well inland, and there are other areas of mangrove that are isolated and dead under too exposed and too saline conditions. In the small bay areas along the north coast *Rhizophora*, *Laguncularia*, and *Avicennia* comprise the swamps. None of these species has developed extensively nor are the areas of swamp large. Associated with the mangrove

in drier areas are specimens of *Thespesia populnea*, *Picrodendron macrocarpum*, *Suriana maritima*, and *Amyris elemifera*. Behind the mangroves may be shallow flats covered now with *Batis*, *Sesuvium*, *Salicornia*, and other halophytes. In among the mangroves and elsewhere along the northern coast of Beata are large piles of conch shells. Some of these appear quite old, others more recent. Krieger (l.c.) has mentioned these piles as composed of pure *Strombus gigas*.

The most interesting vegetation on Beata occurred on the central plateau area that Ostenfeld and Wetmore found too difficult to penetrate. Their descriptions of the area, however, are good. The rock surface is almost smooth in places, while in other regions the surface has become badly eroded into sharp edges so characteristic of southern coastal outcrops of limestone on other islands. This is the dogtooth limestone of the Antilles. Ostenfeld noted the peculiarity of this limestone, that is, its metallic ring when struck. Smaller rocks actually ring when hit. The surface of the plateau shows signs of crustal adjustment, with cracks of varying sizes making progress on foot difficult. Crevices eight to ten feet wide were common, and some of these extended approximately sixty feet or more down into the surface. Compression of the island apparently caused piling of large blocks of limestone in other places. Small fractures were evident, and many of these showed additional weathering or erosion due to root action by plants. These smaller cracks had narrow openings but widened downward in contrast to the large crevices, which tapered downward.

The vegetation of this limestone plateau area was complex in its composition (FIG. 5). It is best described as a thorn shrub. The species comprising the vegetation were numerous. While the area seemed barren of flowers or fruit, by careful search the majority of the dominant plants were collected in either flower or fruit and could be identified. One very common tree, assigned to the Leguminosae in the accompanying list, could not be found in fertile condition and remains unidentified. The impression one carries from work on the vegetation of the plateau is that of a thorn-riddled shrub growth. The spiny trunks of *Opuntia moniliformis* were most foreboding in appearance and in the hazard they presented (FIG. 6). Lesser spines occurred on the branches or leaves of *Malpighia setosa*, *Securinega acidoton*, *Guettarda stenophylla*, *G. xanthocarpa*, *Cryptorhiza haitiensis*, *Malpighia domingensis*, *Reynosia cuneifolia*, *Isodorea leonardii*, *Randia parvifolia*, *Hippomane spinosa*, *Trichilia cuneifolia*, *Cameraria angustifolia*, *Caesalpinia anacantha*, and *Cephalocereus polygonus*. In addition the poisonous properties of *Comocladia dodonea*, *C. mollifolia*, *Metopium brownei*, *M. toxiferum*, *Jatropha hernandifolia* and *Hippomane spinosa* were well known, and these plants, too, had to be avoided.

Nowhere on the island did I see trees of fifty to eighty feet as mentioned in the coastal survey report of 1868. The tallest plants were specimens of *Haitiella ekmanii* which stood out in the profile of the forest canopy. These are the "thrinax-like plants" mentioned by Ostenfeld. The largest trees on the island were *Sarcomphalus domingensis*, *Coccoloba pubescens*, *C. diversifolia*, *Bursera simaruba*, and *Ficus populnea* var. *hispaniolae*. A

single specimen of *Clusea rosea*, also one of the more massive plants on Beata, was seen. Around these few conspicuous plants the vegetation consisted of a dense growth of smaller trees and shrubs, much branched and forming an intertwined canopy of branches six to ten feet above the ground. Many of these plants were microphyllous or had leathery shiny leaves. Broad-leaved plants such as *Ulrichia beatensis* were few. *Comocladia dodonaea* and *C. mollifolia* appeared to be the most numerous. *Cordia buchii* and *Tabebuia ostenfeldii* in full flower presented the most color. The other common species were *Malpighia setosa* and *M. domingensis*, *Capparis flexuosa*, *Krugiodendron ferreum*, *Schoepfia obovata*, *Randia parvifolia*, *Exostemma caribaeum*, *Elaeodendron xylocarpum* (extremely variable in leaf size and shape), *Plumeria obtusa* (also extremely variable), *Securinega acidoton* and *S. neopeltandra*, *Amyris granulata*, *Isodorea leonardii*, *Trichilia cuneifolia*, *Reynosia cuneifolia*, *Samyda pubescens*, *Guettarda xanthocarpa* and *G. stenophylla*. *Opuntia moniliformis* was the only cactus seen in the shrub thickets. Herbaceous growth was conspicuously lacking throughout the interior of the island. *Setaria setosa* was the only grass found in the woodland. *Euphorbia hepatica* and *Commelina diffusa* occurred on the rocks or in pockets of soil. *Zephyranthes bifolia*, a bulbous plant, occurred in small pockets. This plant was not in flower at the time I visited the island, but transplanted bulbs later flowered at Barahona and in the greenhouse in Cambridge. The absence of herbaceous growth was as conspicuous as the extensive development of vines. Much of the progress through the interior was possible only with the continuous stroking of a machete. *Galactia dictyophylla*, *Mesechites repens*, five species of *Cissus*, *Stegnosperma cubense*, *Paullinia jamaicensis*, *Aristolochia bilobata*, and *Chiococca alba* were rampant. Equally troublesome to the foot traveler was the accumulation of dried leaves on the ground. Apparently decay occurred very slowly, for the leaves were deep in many places, and as they hid not only the rough dogtooth surface of the limestone but also the small depressions and many crevices, progress had to be made cautiously.

Epiphytes in general were few in the thorn shrub area. *Tillandsias* were relatively abundant in a few places but generally scarce when compared with a comparable location elsewhere in Barahona province. Only two species of orchids were found, and these occurred only on the very low branches or the prostrate trunks, as described by Ostenfeld.

Six and a quarter miles to the south of Beata is the island called Alta Vela, occasionally spelled Alto Vela (FIG. 7). From a botanical point of view this island was less interesting than Beata, but historically Alta Vela is better known and has played an often forgotten role in American history.

Alta Vela Island was discovered by Columbus on August 20, 1494. As J. B. Thacher (*Christopher Columbus* 2: 336-7. 1903) describes the event, Columbus "anchored at a small island, or rather a rock which rises singly out of the sea opposite to the long cape stretching southward from the center of the island, to which promontory he gave the name of Cape Beata.

The rock at which he anchored had an appearance at a distance of a tall ship under sail and he called it Alta Vela. Several seamen were ordered to climb the rock to watch out for the two lost ships of his squadron. Descending from the summit the sailors killed on the island of Alta Vela eight sea wolves which were sleeping on the sands, knocked down many pigeons and other birds with sticks and took others with their hands; for in this unfrequented island the animals seemed to have none of the wildness and timidity which is produced by hostility of man."

As Alta Vela, like Beata, was destitute of natural water supplies, few ships stopped there except for food or firewood, and no evidence can be found in the literature that the island was ever occupied by other than transients. It is a small island about three quarters of a mile long and a half-mile wide composed originally of a "remarkable bell-shaped hill, the summit 500 feet above sea level." Alta Vela Island almost became a possession of the United States in the middle of the nineteenth century, and the dispute over the ownership of it forms an interesting part of American political history. The story is told in detail in the Senate Executive Document No. 38 of the second session of the Fortieth Congress (1868), in Document No. 17 of the third session of the Forty-first Congress (1871), and reviewed in "The United States and Santo Domingo 1798-1873," pages 287-337, by Charles C. Tansill. I am quoting liberally from these documents in summarizing the history of Alta Vela.

The United States Congress, on Aug. 18, 1856, passed a law to legalize claims of American citizens to unoccupied islands with guano deposits. The law stated, "When any American citizen chances to discover a deposit of guano on any island, rock or key not within the lawful jurisdiction of any other government and takes peaceful possession thereof, and occupies the same, such island, rock or key may, at the discretion of the President, be considered as appertaining to the United States." As soon as practicable the claimant should give notice to the Department of State of such discovery and occupation describing the island, rock or key and the latitude and longitude thereof as near as may be, and showing that such possession was taken in the name of the United States and should furnish satisfactory evidence to the State Department that such island was not at the time of discovery thereof or the taking possession of and occupation thereof by the claimant in the possession or occupation of any other government. After these conditions were met the discoverer might at the pleasure of Congress be allowed "exclusive rights of occupying such island, rocks or keys for the purpose of obtaining guano and of selling and delivering the same to citizens of the United States."

It was with this law in mind that a schooner owned by the Baltimore firm of Patterson and Murguiendo took possession of Alta Vela on Feb. 23, 1860. In May and June the Secretary of State and the State Department of Buchanan's administration were notified that a claim to the uninhabited and unclaimed island was made for the United States. Mining operations were carried on, and when a Dominican vessel stopped at the island in September of that year, its officers were given a sample of the guano. In

early October the Dominican government ordered the Americans to leave the island, which they refused to do, and on the twenty-third of October a vessel of the Dominican government landed troops who arrested the workers and removed the mining equipment. These workers and a company representative sent to obtain their release were held prisoners in Santo Domingo city for nearly thirty days, in spite of promises of safe conduct. The company protested the action to the American Secretary of State. Buchanan's term expired, Johnson became president, and Seward was appointed Secretary of State. Black, the former Secretary, was hired as counsel for the protesting firm. Seward at the time was negotiating with the Dominican government for the use of Samana Bay at the northeast corner of Hispaniola as a United States naval base and was not anxious to force the claim of the previous administration regarding Alta Vela. In fact Seward was thought to be guilty of duplicity when he informed a competing firm, Webster & Co. of New York, that in his opinion the territory under question belonged to the Dominican government. An intimate friend of Seward was found to have a large interest in Webster & Co., and the rage against Seward and Johnson increased when it was learned that the Dominican government had given permission to the Webster company to remove guano from Alta Vela. Patterson and Murguiendo Co., the original claimant to the Alta Vela guano, reported to the State Department that at the current rate of mining and exporting at two thousand tons per month, the guano would soon be exhausted. When the House of Representatives, a few months later on Feb. 24, 1868, agreed on a resolution of impeachment against Johnson, the events which had occurred in Seward's handling of the Alta Vela dispute ranked high. The House Committee on Foreign Affairs, which investigated the dispute, reported, "We are compelled to say that the case is too clear to allow of the least hesitation. Santo Domingo was guilty of an inexcusable outrage upon the rights of the memorialists and a gross insult to the United States." In May of 1869 an appeal was made to Hamilton Fish, the new secretary of state under Grant, for a decision in the case. Finally in May of 1870 Fish reported to the attorneys for Patterson and Murguiendo that all of the documents and pertinent correspondence had been placed before President Grant, who after due consideration determined that no sufficient reason appeared for reconsidering the conclusions heretofore reached.

With that decision Alta Vela dropped from the news. Apparently in due time the guano deposits were mined out. From information and estimates which appeared in the Senate Executive Documents, Alta Vela once contained fifteen thousand tons of guano. An analysis of this material showed it contained 29.16% phosphoric acid and 70.84% lime.

Apparently the mining operation forced the sea birds to change their habits, for no large numbers of them roost on Alta Vela today. The scars of the mining operations on the leeward slopes of the island are still visible, and artifacts of mining still litter portions of the hill (FIG. 10).

Alta Vela, with no wood, water, or fertile soil, remains a desolate outpost. Today a single house and a few small supply buildings take care of the

needs of a lighthouse keeper. The lighthouse at the summit of the hill represents one of the southernmost beacons of the Greater Antilles (FIG. 9).

For the botanist visiting Alta Vela today there is little of interest. The island is bounded by severe wave-washed and undercut cliffs (FIG. 8).

Around the island the bottom drops off sharply, and within a short distance of the shore it consists primarily of boulders offering poor if any anchorage in the heavy seas that continuously wash the island. Landing from the destroyer escort which provided transportation for me proved hazardous, and in fact the vessel stayed under power to hold its position during my visit to the island. Apparently previous occupants of the lighthouse keeper's position tried to grow vegetables and crops of cotton on the slopes on the leeward side. The current keeper informed me he had learned this to be futile, for the lack of sufficient moisture and the frequent dousings with salt spray killed off all his attempted crops.

Alta Vela today has primarily a weedy vegetation. The few woody plants which occurred on the island were located in ravines, primarily on the leeward side of the island (Fig. 10). Those shrubs struggling for existence on the crest of the hill or on the windward side were severely wind-blown and malformed (FIG. 9). These woody plants were few. *Capparis flexuosa* and *C. cynophallophora*, *Ficus populnea*, *Pithecellobium unguis-cati* and *Duranta repens* represented the largest woody plants. *Morinda royoc*, *Iresine angustifolia*, *Eupatorium corymbosum*, and *Sesbania sericea* were the most common plants of low stature. The coastal or flatland areas were dominated by weedy species. In fact the list of twenty species found on Alta Vela and not on Beata would show only pan-Caribbean, if not pan-tropical weeds. There are no evidences of even interesting species of limited range found on the island.

Many of the areas, particularly the mined-out areas on Alta Vela, appeared from the sea to be grassy meadows (FIG. 10.). These were deceptive even from nearer by. The grasses and sedges giving this impression, *Paspalum bakeri*, *P. adspersum*, *Setaria geniculata*, *Cyperus compressus*, *Fimbristylis spathacea*, formed dense stands one to three feet high. However, mixed in with these grasses and hidden by them were extensive mat-like growths of *Opuntia antillana*. *Opuntia dillenii* was common around the edges of these swales. On the exposed rocky outcrops at the sea-cliff margin of the island the vegetation is stunted and consists of the usual halophytes of such areas, *Lithophila muscoides*, *Portulaca oleracea*, *Talinum paniculatum*, *Iresine angustifolia*, and *Sesuvium portulacastrum*. Common in such locations, however, is the turk's cap cactus, *Cactus lemari*.

Alta Vela, by contrast to Beata, has a flora consisting entirely of a woody pauperous vegetation. Whether the island ever had the interesting flora found on Beata is impossible to speculate. Probably its environment was such that shelter was lacking, and only the most hardy of Caribbean plants could grow. Mining operations may have removed some of the vegetation from the sheltered leeward slopes, but the abundance of birds

necessary to produce the guano may also have played a role in the development of the present weedy vegetation.

The vegetation on Alta Vela offers little information regarding the affinities of the flora of the southern coast of Hispaniola, particularly when contrasted with that of Beata.

Beata Island possesses a flora consisting of 118 genera and 168 species, as based on the collection records of Ostenfeld and Howard. The vast majority of the species on Beata are wide-ranging species, but thirty-five of them, representing twenty per cent of the flora, are species of limited distribution and contribute information regarding the affinities of this islet. In addition, three good species are to be currently regarded as endemic to Beata. These are *Ulbrichia beatensis*, *Tabebuia ostenfeldii*, and *Galactia dictyophylla*. One species, *Euphorbia hepatica*, is known elsewhere only from Navassa Island. *Guettarda xanthocarpa*, *G. stenophylla*, *Amyris granulata*, and the hybrid between *Coccoloba uvifera* and *C. pubescens* are known only from the vicinity of Trujin on the Barahona peninsula. *Salicornia bigelovii* has also been collected by Ekman on Gonave Island but is not known from the main island of Hispaniola. Two species, *Elaeodendron ehrenbergii* and *Antirrhoea elliptica*, have been previously collected only in the Cul de Sac, with the latter known only from Isla de Cabritos in Lake Enriquillo.

In general the relationship of the vegetation of Beata Island is with the dry-land shrub vegetation extending from southeastern Haiti through the Barahona peninsula into the Enriquillo valley and eastward to the vicinity of Azua. There is no indication in the Beata flora of affinities with the vegetation of the western end of the southern peninsula of Haiti, a floristically distinct area frequently pointed out by Ekman. Geologically, as well as botanically, Beata appears to be a fragment of recent fracture from the Barahona peninsula.

A comparison of Beata Island with the other islands intensively studied by Ekman reveals that for its small size and lack of topography Beata has indeed a very interesting vegetation. Beata ranks in size with Navassa (*Arkiv för Botanik* 22A (16): 1-12. 1929). The number of species found on Beata is greater, the percentage of endemics about equal; the percentage of introduced or weedy species is much less and the number of interesting species of limited range much higher. The larger size of Gonave Island and the greater range of topography, coupled with its location, have produced a much larger flora, 928 species, than that found on Beata (*Arkiv för Botanik* 23A (6): 1-73. 1930). The same is true of Tortue Island, which has 889 species (*Arkiv för Botanik* 22A (9): 1-61. 1929). Gonave, Tortue, and Navassa are reported to have a soil developed in all or parts of the islands. All seem to receive sufficient rainfall to support the diversified vegetation present. All are in the paths of prevailing winds and currents which would aid the introduction of additional species of plants from the mainland of Hispaniola. Beata stands by contrast. No accurate rainfall records are available for Beata. According to the naval personnel stationed on the island the rainfall is very slight. The catchments estab-

lished on the buildings on Beata do not provide sufficient rainfall for the personnel, and water must be imported. The accumulation of leaves on the surface of the plateau supports the conclusion that sufficient moisture is not available for decay of vegetation. Interestingly, termite action was not noticed on the island. The lack of soil on Beata has prevented the development of a fern flora or of extensive herbaceous growth. The location of Beata, south of the Barahona peninsula, has prevented the introduction of many species from the mainland of Hispaniola by natural transport. Particularly striking in the Beata flora was the complete lack of certain major groups of plants, such as the ferns, and the few examples of epiphytes and palms seen. Families and genera of flowering plants expected in similar dry thorn shrub areas of Hispaniola were also lacking. In particular the absence of members of the Piperaceae, Loranthaceae, Flacourtiaceae, Myrsinaceae, Sapotaceae, Labiatae, Solanaceae, Rutaceae, and Acanthaceae was noted. Characteristic genera such as *Pilea*, *Zanthoxylum*, *Trema*, *Phyllostylon*, *Maytenus*, *Casearia*, *Sideroxylon*, *Bumelia*, *Acacia*, and *Mimosa* were missing from the flora. Additional work on the flora of Beata may be expected to produce additional distributional records, but such work must be accompanied by an examination of the vegetation from Lago Trujin to Punta Beata for comparison. The succession of plant life in the abandoned salt pans should be followed for information on replacement of vegetation in dry-land areas. Nowhere could a study of the development of such a high percentage of toxic and spiny plants as related to the factors of their environment be better attempted.

A LIST OF PLANTS OF BEATA AND ALTA VELA ISLANDS

HYDROCHARITACEAE

Thalassia testudinum Koenig. Beata; *Ostenfeld s.n.*, Howard by observation.—A marine plant particularly common off the north shore in shallow water.

GRAMINEAE

Cenchrus brownii R. & S. Alta Vela; *Howard 12474*.

Cenchrus myosuroides H.B.K. Alta Vela; *Howard 12464*.—Found near the crest of the hill. The stems prostrate, to six feet long.

Cenchrus pauciflorus Benth. Beata; *Howard 12419*.—Plant of open sandy area at the northwest corner of the island. Stems prostrate, radiating.

Panicum adspernum Trin. Alta Vela; *Howard 12462*.—A prostrate plant with radiating branches.

Panicum maximum Jacq. Beata; *Ostenfeld* by observation, *Howard 12389*.—A common grass in areas around bays and old salt pans.

Paspalum bakeri Hackel. Alta Vela; *Howard 12480*.—A common clump grass, perhaps the most abundant and dominant plant on old

guano mined areas. Previously collected on Inagua, Cuba and Barbuda. This is the first record from Hispaniola.

Setaria geniculata (Lam.) Beauv. Alta Vela; *Howard 12471.*

Setaria setosa (Sw.) Beauv. Beata; *Howard 12493.* — Perhaps the only grass growing on limestone in brush thickets. Plants few, scattered.

Sporobolus domingensis (Trin.) Kunth. Beata; *Ostenfeld 330*, Howard by observation. A beach grass dominating sandy areas in the northeast corner of the island. Sterile in August.

Sporobolus pyramidatus (Lam.) Hitch. Alta Vela; *Howard 12460.* — A rare plant; only one specimen seen on the lee side of the island.

CYPERACEAE

Cyperus compressus L. Alta Vela; *Howard 12465.* — An uncommon sedge found on rocks near the lighthouse.

Cyperus nanus Willd. Beata; *Howard 12400.* A single specimen found on the limestone benches near the coast.

Cyperus planifolius L. C. Rich. Beata; *Howard 12447.* Alta Vela; *Howard 12467.* A clump-forming plant found on sand, especially in swales on Beata. On Alta Vela this species is more common, being found in large colonies on the leeward slopes where guano had been mined. This area has been burned frequently, and the charred bases of these plants give the hill a blackened appearance from the sea.

Fimbristylis spathacea Roth. Alta Vela; *Howard 12466.* — A sedge occurring from sea level to the crest of the island. More abundant at the lower elevations.

Mariscus bruneus (Sw.) Clarke. Beata; *Ostenfeld 318, 339.*

Remirea maritima Aubl. Beata; *Howard 12427.* — This unusual sedge was particularly common in the grassy areas in the northeast corner of Beata Island on sand at the edge of limestone. The white bracts cause the plant to be conspicuous even from a distance. The species has been reported previously only from the vicinity of Barahona on Hispaniola. One locality record is known from Puerto Rico. The species is more common in Trinidad, South America, and Africa.

BROMELIACEAE

Tillandsia balbisiana Schl. Beata; *Howard 12349.* — An epiphyte in the shrub thickets.

Tillandsia circinnata Schl. Beata; *Ostenfeld 327.*

Tillandsia recurvata L. Beata; *Howard 12508.* — A common epiphyte found only on the western side of the island on shrubs in the lee of the cliff face.

Tillandsia usneoides L. Beata; *Ostenfeld 315, Howard 12380.* An epiphyte of general occurrence.

Tillandsia utriculata L. Beata; *Howard* 12374. — The largest epiphyte found in the interior of the island.

COMMELINACEAE

Commelina diffusa Burm. f. Beata; *Howard* 12494. — A fleshy herb found on the limestone in the shrub area away from the coast.

PALMAE

Haitiella ekmanii (Burret) Bailey. Beata; *Howard* 12369, 12420. — Apparently the only palm on Beata Island. At the northern end of the island this species is quite abundant in windswept shrub formations, averaging here ten feet in height. Toward the southern end and in the interior in the shrub thickets the palm reached forty feet in height. This species was known previously only from the southern peninsula of Haiti at Anses-à-Pitre on Morne Savane Lafleur (Contrib. Gray Herb. 165: 5-9. 1947).

AMARYLLIDACEAE

Zephyranthes bifolia (Aubl.) Roem. Beata; *Howard* 12499-a. — A bulbous plant occurring in cracks and crevices in the limestone in the interior of Beata. The plant was in sterile condition in August when collected. The bulbs collected were planted and flowered in November in Barahona, while others flowered in March in Cambridge, Mass., allowing positive determination. The species is relatively common on limestone in Hispaniola but is not known elsewhere to me at such a low altitude.

ORCHIDACEAE

Laeliopsis domingensis Lindl. (*Broughtonia domingensis* Rolfe). Beata; *Ostenfeld* s.n., *Howard* 12402, 12428. — An epiphyte of the shrub area, widespread on the island. Ostenfeld notes that these plants occur primarily on the lower branches or trunks of the shrubs. I can verify that this seems to be the pattern of occurrence of the species on the island.

Oncidium intermedium Bert. Beata; *Howard* 12518. — Locally abundant in the thorn shrub areas along the western coast of the island.

ULMACEAE

Celtis trinervia Lam. Beata; *Howard* 12372. — Trees of fifteen feet with green fruit. In the thorn shrub areas on limestone.

MORACEAE

Ficus populnea Willd. var. *hispaniolae* Urb. Beata; *Howard* 12516. Alta Vela; *Howard* 12482. — A twenty-foot tree on Beata Island occurring in the thorn shrub. The striking dark green foliage makes

this plant conspicuous in the thickets. On Alta Vela this species is generally found on the windswept eastern slopes, where plants from one to fifteen feet tall were seen.

URTICACEAE

Rousselia humilis (Sw.) Urb. Beata; *Howard 12375*. — One of the few terrestrial herbs in the limestone areas.

OLACACEAE

Schoepfia obovata Wr. Beata; *Howard 12383*. — An exceedingly common shrub of thorn thickets. Plants occur to eight feet tall.

ARISTOLOCHIACEAE

Aristolochia bilobata L. Beata; *Howard 12366*. — A sterile vine with distinctive foliage.

POLYGONACEAE

Coccoloba diversifolia Jacq. Beata; *Howard 12361*. — A common tree fifteen to twenty-five feet in height in thickets on limestone.

Coccoloba pubescens L. Beata; *Howard 12352*. — One of the largest trees on Beata Island reaching twenty-five feet in height. It occurs on the limestone from the benches of the west coast to the center of the island.

Coccoloba subcordata (DC.) Lind. Beata; *Howard 12488*. — Prostrate or ascending shrubs occurring on the limestone plateau.

Coccoloba uvifera L. Beata; *Howard 12489*. Alta Vela; *Howard 12453*. — Trees reaching fifteen feet are found along the coast in sandy areas.

Coccoloba uvifera × **C. pubescens**. Beata; *Howard 12499*. — This new hybrid was first discovered south of El Caiman on Barahona peninsula, where several stands of the plant had developed between colonies of the parents. The hybrid is a true intermediate with the leaf shape of *C. uvifera* but the venation and texture of *C. pubescens*. The fruits were all sterile but of the size and shape of those of *C. uvifera*. Only a single specimen, eight feet tall, was found on Beata at the southern end of the sandy strip which occurs on the northwest corner of the island.

CHENOPodiACEAE

Atriplex pentandra (Jacq.) Standl. Beata; *Howard 12451*. — A single plant was found on the rocks of the coastal bench. Moscoso lists this plant without specific location in his catalogue of plants from the island. This is the first specimen of this species I have collected in Hispaniola.

Salicornia bigelovii Torr. Beata; *Howard 12442*. — A relatively abundant species mixed with *Batis* and *Sesuvium* along the lagoon

near the salt pans. Moscoso does not record this species from Hispaniola although Ekman collected it on Gonave Island near Trois Louis. Ekman reported the species was not found on the mainland, although it is found on the Atlantic coast of the United States and in Cuba. This collection represents the second record from Hispaniola, but again from an island, not the mainland.

AMARANTACEAE

Amaranthus gracilis Desf. Alta Vela; *Howard* 12458.—This species occurred as a weed in an old field on Alta Vela. Moscoso does not list it in his Catalogue, although I have now collected the taxon at Manzanilla and in the Enriquillo basin. Ekman found the same species on Gonave.

Celosia nitida Vahl. Beata; *Ostenfeld* 320.

Iresine angustifolia Euph. Alta Vela; *Howard* 12456.—The species occurs as a weed on the area disturbed by guano mining.

Lithophila muscoides Sw. Beata: *Ostenfeld* 345, *Howard* 12426. Alta Vela, *Howard* 12461.—On both Beata and Alta Vela this species was a prostrate plant of limestone coastal benches.

NYCTAGINACEAE

Boerhaavia caribaea Jacq. Beata; *Howard* 12487. Alta Vela; *Howard* 12472.—A sporadic weed occurring primarily in the grassy areas.

Neea subcoccinea Heimerl. Beata; *Howard* 12379.—Characteristic shrub of limestone plateau. Plants to eight feet tall with widespread branches. This species is apparently endemic to Barahona province and has been recorded previously only from that vicinity.

BATIDACEAE

Batis maritima L. Beata; *Howard* by observation.—A common woody perennial along the lagoon and edges of the salt pans on Beata.

PHYTOLACCACEAE

Rivina humilis L. Alta Vela; *Howard* 12476.—Plants to two feet tall were relatively common in the sheltered areas on Alta Vela.

Stegnosperma cubense A. Rich. (*Stegnosperma halimifolium* auct.). Beata; *Ostenfeld* 319, *Howard* 12507.—A trailing or scrambling fleshy-stemmed to woody bush quite common at the edge of the sand and limestone on the western coast of Beata Island. Moscoso does not give a specific location for the occurrence of this species in Hispaniola. D. J. Rogers (Ann. Mo. Bot. Gard. 36: 475. 1949) cites two collections by *Fairchild*, numbers 2605 and 2606, from Beata Island. He likewise records collections by Ekman from Massif des Cahos, Barahona, and Sierra de Ocoa.

Playfair in his *Geography* (6: 625. 1814) states, "On Beata the soil is good and was once in a state of cultivation. Till the fall of Santo Domingo, it was the great resort of French privateers." As recently as 1918 Otto Schoenrich (*Santo Domingo, A Country with a Future*, pages 113-114) described Beata as follows: "The island is covered with dense forests in which wild cattle abound. During the sixteenth and seventeenth centuries the island was a convenient resort for the pirates that infested the Spanish main; at one time it is said to have contained fine plantations, but at the present it is only occasionally visited by Dominican or Haitian fishermen." These reports are hard to believe in the light of a present-day examination of the island.

Only two modern visits to the island have been made by botanists, to the best of my knowledge, although zoologists and anthropologists have been there more frequently. The Danish Oceanographical Expedition with the steamer Dana explored the warmer parts of the Caribbean Sea and the Gulf of Panama in 1921 and 1922. Strong trade winds forced this ship to seek shelter on the west side of Beata on Feb. 22, 1922, and apparently it was anchored in essentially the same spot that Columbus chose. One of the botanists aboard this ship was C. H. Ostenfeld, who took advantage of the two-day lay-over to collect marine algae and to make a short visit ashore. The specimens of flowering plants which he collected were described by Urban in the *Dansk Botanisk Arkiv* 4(7): 1-37. 1924. Ostenfeld reports that they landed at the northwest corner of the island. "No inhabited human dwellings were to be seen but a grassy area mostly covered with *Panicum (maximum?)* and scattered cotton plants shew that formerly culture had existed here." Ostenfeld indicated throughout his brief report that the island was a difficult place to travel on or to collect plants.

Between 1929 and 1934 the expeditions sponsored by Allison Armour on his yacht the Utowana made several stops at Beata Island. I have been unable to date these specifically and have been able to locate only four records of plants collected during these visits. Thomas Barbour in his privately printed book, "Allison Armour and the Utowana," refers to his visits to Beata aboard the Utowana in the spring of 1929 and again in April of 1934. In 1932 the Utowana apparently made another visit to Beata Island, for one of the plants collected by the botanists aboard, David Fairchild and P. H. Dorsett, proved to be new and was described as a new genus *Armouria* (= *Ulbrichia*) of the Malvaceae. Mr. Harold Loomis, director of the Plant Introduction Station of the U. S. Department of Agriculture at Coconut Grove, Florida, was also on this expedition and introduced seeds of this new genus for cultivation in Florida. David Rogers, in his revision of *Stegnosperma* of the Phytolaccaceae, cites two other collections from Beata Island by these men. No collectors' lists or field books have been located for this expedition, although a gap of twelve numbers occurs between the *Stegnosperma* and *Armouria* collections.*

* After this paper was prepared I had the opportunity of visiting Mrs. David Fairchild at Coconut Grove and Mr. Harold Loomis at the Plant Introduction Station, also in Coconut Grove, Florida. Mrs. Fairchild kindly made Dr. David Fairchild's

Herbert W. Krieger, in an article on the Culture Sequences in Haiti (Smithsonian Institution Publication 3134: 113-124. 1932) refers to Beata Island and publishes a photograph of the shell mounds of pure *Strombus gigas* on the island. I was unable to determine the source of this photograph or the nature of the expedition. Alexander Wetmore visited Beata for a time in the spring of 1931, as he reports in the Smithsonian Institution Publication 3134: 45-54. 1932. He and his party hired a sail-boat and sailed for Barahona. Wetmore illustrated a small settlement called Ocrik on Beata Island and reported that his party stayed in one of the houses. The settlement at Ocrik was not in evidence during my visit in 1950. Wetmore's description of the vegetation indicated that it has changed little since Ostenfeld's visit, as he reports, "Thorny bushes, trees and vines growing from the scanty soil accumulated in crevices in the rock form a jungle so dense that it may be penetrated only along trails cut laboriously into the interior."

Thus I seem to be the first botanist to make a deliberate attempt to visit this island and to make comprehensive collections. I am not satisfied

field notes for this expedition available to me for study. She was also able to refer to photographs made on Beata Island, and her recollections of the Utowana's stay at Beata were most pleasant and helpful. Mr. Loomis, also, was able to refer to field books for information on his collections as a member of the party, and he had some excellent photographs of the area. From the field notes of Dr. Fairchild and Mr. Loomis I was able to prepare a numerical list of their collections on Beata, and Mr. E. C. Leonard of the U. S. National Herbarium has been most helpful in checking the herbarium for these specimens. He was not able to locate all of them, and in some cases in the following list field determinations are given. I am most indebted to Mrs. Fairchild, Mr. Loomis, and Mr. Leonard for their assistance.

The Utowana, with Fairchild, Dorsett and Loomis as botanists, stopped at Beata Island on January 17th and March 22nd, 1932. Only a single collection was made by Loomis on the latter date. He collected six numbers on the island on January 17th. Number 15 was identified in the field as *Coccothrinax ekmanii*. This is currently called *Haitiella ekmanii*. The specimen was not located in the National Herbarium. Numbers 16, 17, 18, 19 and 20 collected by Mr. Loomis were species of *Gossypium*. No material could be located at the National Herbarium. On March 22, 1932, Mr. Loomis collected a single number, 94, representing *Pseudophoenix saonae*. Mr. Loomis stated that Cook was in doubt regarding this identification at the time, but Mr. Leonard reports that a specimen so identified is in the National Herbarium.

The following collections by Fairchild and Dorsett were all made on Beata Island on January 17, 1932. Specimens present in the National Herbarium are indicated with an asterisk. All other names represent field identifications from Dr. Fairchild's field notebook: 2603, *Guilandina ovalifolia*; 2604, *Opuntia moniliformis*; 2605, *Stegnosperma cubense**; 2606, *Stegnosperma cubense**. Number 2606 in Fairchild's field notebook is identified as *Zanthoxylum* sp. A specimen with the same number is cited by Rogers and is in the National Herbarium as *Stegnosperma cubense*. No. 2607, *Capparis flexuosa**; 2608, *Plumeria obtusa* var. *obtusa**; 2609, *Tribulus cistoides*; 2610, *Bromelia* sp.; 2611, *Exogonium eriospermum**; 2612, *Canavalia maritima**; 2613, *Maytenus reynosoioides**; 2614, *Coccothrinax ekmanii*; 2615, *Rhynchosia minima**; 2616, *Indigofera suffruticosa**; 2617, *Ulbrichia beatensis*.

One addition can be made to the list of species from Beata Island given in this paper, on the basis of the Fairchild and Dorsett collections available in the National Herbarium. *Rhynchosia minima* (L.) DC. should be added to the Leguminosae.

that I have mastered the flora, however, and wish to pay a return visit at a different season.

Beata today appears from the sea to be a low flat island (FIG. 1). It is a large block of limestone which apparently has been tilted by coastal adjustments. The island is approximately five miles long and three miles broad, according to the skipper of the "27 de Febrero." It is shaped like a wedge of pie, broadest at the northern end and slightly rounded at the south. The north end (FIG. 3) is a sandy plain, at sea level, interrupted by shallow bays now filled with marine succulents and mangroves. The eastern side, likewise, is mostly level with the sea. The greatest elevation is approximately three hundred feet, at the southwest corner. The entire western side of the island shows a series of wave-cut benches with an escarpment of fifty to two hundred feet running from the coast at the north to a point well inland at the southern end of the island (FIG. 2). The surface of this major block is essentially flat, tilting slightly to the northeast. It appears, therefore, that this block of limestone has been tilted by sinkings on the northern and eastern edges. The first crustal adjustment was the most severe, but evidence of at least two other benches on the western side indicates subsequent changes in the attitude of the limestone.

Ostenfeld described Beata as "consisting of rocks of volcanic origin, being more or less horizontally lying light-colored lava-beds. There is often a short terrace of bare lava-rock; from it the inclination towards the water is nearly vertical, often interrupted by fissures and small caves into which the waves break with much noise." He made mention of the lush green vegetation on the coastal sand, accumulations of *Sesuvium portulacastrum*. Inland from the shore Ostenfeld noted that the most favorable place for the vegetation was in the lee of cliff faces. Above this was the flat but faintly sloping plateau. Ostenfeld climbed the cliff face and found on top a plateau covered with much wind-blown vegetation of low, many-branched trees. He comments, "Many lianas interweave the small trees and numerous cacti and other shrubs are scattered amongst the trees. It was very difficult to make a way through this vegetation, also because it was without any shade at all and extremely hot. The soil surface was nearly bare lava-rock which gave a sonorous sound when we walked on it, and loose soil was found in small holes and deepenings. It was really quite astonishing to find such a comparatively dense plant cover on this rocky surface." Further in his report Ostenfeld relates, "The difficulty in walking in this shade-less vegetation of 3-6 meters high trees, hindered by lianes and the stinging Cacti and other thorny shrubs, prevented me from proceeding far into it. At a distance some slender palms—*Thrinax* or another genus of the same appearance—rose above the low trees, but I could not reach into them. Therefore, I turned back, climbed down the steep cliff-wall to the shore-terrace and examined the vegetation sheltered by the wall." Ostenfeld concludes his report by stating, "Taken as a whole the vegetation shows that the climate must be very dry and probably the rainfall is very low, which together with the strong and constant wind produces the pronounced xeromorphism; but of course no meteorological

data are available. My visit was in winter which probably is the rainy season, but one did not get much impression of that, the only sign may be the shooting of new leaves on some of the *Bursera*-trees and the *Guaiacum*-shrubs."

I had the opportunity during my visit there to cover much more of the island than did Ostenfeld and to penetrate deeper into the spiny shrubland. I established as a starting point for most work the sandy beach area in the northwest corner of the island. This is the location that Ostenfeld mentioned where he saw a number of cotton plants, indicative to him of former cultivation. From this point I worked as far southward as possible on the western side of the island. I also penetrated directly eastward from that starting point and made a long trip around the northern end of the island, working due south from the north towards the interior, later continuing around the northern end and down the eastern side to a point beyond the abandoned salt ponds. Later, with the assistance of the destroyer escort, several landings were made along the west coast at favorable places, and penetration was made directly inland to the cliff face and onto the plateau in three locations.

Sea-level shore lines of Beata Island are of three types: sand, low limestone shelves or benches, and mangrove swamps. Small sandy beaches are common on the west coast (FIG. 2). One of these in the northwest corner of the island is now occupied by several buildings which form the on-shore headquarters of the naval units stationed at Beata. The sailors have attempted to grow some crop plants, but with little success, due to the low nutrients present in the sand and the lack of rainfall. With no accumulation of fresh water anywhere on the island, except in casual rock depressions, the buildings are used as catchments for rain water for the naval personnel. The largest sandy beach observed occurred on the northern end of the island, where on-shore winds have piled the sand on the outcrops of limestone rock.

The vegetation of the sandy beach areas is of the type found commonly in the Antilles (FIG. 2). *Panicum maximum*, an introduced grass, forms the largest stands of greatest height among the herbs. *Opuntia dillenii* occurs commonly at the edges of the grass. *Sesuvium portulacastrum* forms mats of succulent vegetation in open areas. Scattered and individual plants of *Tephrosia cinerea*, *Cenchrus pauciflorus*, *Cassia buchii*, *C. strigillosa*, *Corchorus hirsutus*, *Stachytarpheta jamaicensis*, *Indigofera suffruticosa*, and *Evolvulus alsinoides* occur on the open sand. Extensive development of the herbaceous vines *Ipomoea pes-caprae*, *Echites umbellata*, *Canavalia maritima*, *Passiflora suberosa*, and *Calonyction tuba* cross the open sand, and *Stegnosperma cubense* is rampant in protected areas near the stands of grass. To the rear of the open sand beaches, and especially in more sheltered areas, *Suriana maritima*, *Colubrina ferruginea*, *Lantana reticulata*, *Capparis flexuosa*, *Amyris elemifera*, *Jacquinia barbasco*, *Canella alba*, and *Caesalpinia anacantha* occur.

The limestone shelves are badly eroded and the surface is described as dogtooth limestone. Near the ocean the vegetation on these coastal shelves

is affected by the salt spray, about as described by Ostenfeld. In general all plants on these shelves are stunted and contorted. *Avicennia nitida*, *Amyris elemifera*, *Conocarpus erecta*, *Ernodea littoralis*, and *Rhacoma crossoptetalum* are the most common woody plants. *Cyperus nanus*, *C. planifolius*, and *Lithophila muscoides* are the most common herbaceous plants on the limestone benches. Further inland on the limestone benches the effects of the salt spray and the wind are less evident, and the vegetation becomes more luxuriant, approaching in composition that of the plateau area. Evidence of repeated tilting of the island can be found on the western side, where several small cliff faces exist before the main break to the plateau is found. Each cliff face shows undercutting due to previous wave action. These small caves are devoid of vegetation and are extremely dry. It is these caves that seem to be the habitat of the rhinoceros iguana (*Cyclura cornuta*) near the sea.

At the northern end of the island the transition from sand to limestone is gradual and migratory due to the wind action of blowing sand from the beaches onto the gently sloping rock (FIG. 3). The typical succulent beach vegetation gives way to extensive stands of grass and sedge and finally to a belt of pure sedge growth at the edge of the limestone. One of the conspicuous areas of the sedge belt near the limestone was composed of a large stand of *Remirea maritima*. The white bracts of this plant attracted the eye from a considerable distance.

The outcrop of limestone rock at the northern end of the island, exposed as it is to strong winds and salt spray, was occupied by an open stand of shrubby plants (FIG. 4). The rock in this region was heavily creviced and broken. Many of the plants found there were rooted deep down in the cracks with only the crown of the plant protruding. The few plants which did root in the small soil pockets on the limestone were strongly wind-blown, often with branches developing only on the leeward side of the plant. A few species, *Clerodendron spinosum*, *Erithalis vaccinifolia*, *Antirrhoea elliptica*, *Strumpfia maritima*, *Borrichia arborescens*, were found in this area alone on the island. The concentration of the palm *Haitiella ekmanii* in this wind-blown shrub zone was also unusual. *Haitiella* was found commonly in the interior of the island on the limestone plateau, but as scattered or individual plants. In the northern shrub zone just mentioned, however, plants of *Haitiella* were clustered (FIG. 4).

The third coastal type of vegetation, the mangrove swamp formation, was also most common on the northern end of the island. The shallow coastal waters and the gradually ascending beach area have combined to produce the type of shore line best suited to mangrove development. Apparently the profile of the shore line has varied in the past, due to shifting currents and deposition and removal of soil. Some of the mangrove formation is now well inland, and there are other areas of mangrove that are isolated and dead under too exposed and too saline conditions. In the small bay areas along the north coast *Rhizophora*, *Laguncularia*, and *Avicennia* comprise the swamps. None of these species has developed extensively nor are the areas of swamp large. Associated with the mangrove

in drier areas are specimens of *Thespesia populnea*, *Picrodendron macrocarpum*, *Suriana maritima*, and *Amyris elemifera*. Behind the mangroves may be shallow flats covered now with *Batis*, *Sesuvium*, *Salicornia*, and other halophytes. In among the mangroves and elsewhere along the northern coast of Beata are large piles of conch shells. Some of these appear quite old, others more recent. Krieger (l.c.) has mentioned these piles as composed of pure *Strombus gigas*.

The most interesting vegetation on Beata occurred on the central plateau area that Ostenfeld and Wetmore found too difficult to penetrate. Their descriptions of the area, however, are good. The rock surface is almost smooth in places, while in other regions the surface has become badly eroded into sharp edges so characteristic of southern coastal outcrops of limestone on other islands. This is the dogtooth limestone of the Antilles. Ostenfeld noted the peculiarity of this limestone, that is, its metallic ring when struck. Smaller rocks actually ring when hit. The surface of the plateau shows signs of crustal adjustment, with cracks of varying sizes making progress on foot difficult. Crevices eight to ten feet wide were common, and some of these extended approximately sixty feet or more down into the surface. Compression of the island apparently caused piling of large blocks of limestone in other places. Small fractures were evident, and many of these showed additional weathering or erosion due to root action by plants. These smaller cracks had narrow openings but widened downward in contrast to the large crevices, which tapered downward.

The vegetation of this limestone plateau area was complex in its composition (FIG. 5). It is best described as a thorn shrub. The species comprising the vegetation were numerous. While the area seemed barren of flowers or fruit, by careful search the majority of the dominant plants were collected in either flower or fruit and could be identified. One very common tree, assigned to the Leguminosae in the accompanying list, could not be found in fertile condition and remains unidentified. The impression one carries from work on the vegetation of the plateau is that of a thorn-riddled shrub growth. The spiny trunks of *Opuntia moniliformis* were most foreboding in appearance and in the hazard they presented (FIG. 6). Lesser spines occurred on the branches or leaves of *Malpighia setosa*, *Securinega acidoton*, *Guettarda stenophylla*, *G. xanthocarpa*, *Cryptorhiza haitiensis*, *Malpighia dominicensis*, *Reynosia cuneifolia*, *Isodorea leonardii*, *Randia parvifolia*, *Hippomane spinosa*, *Trichilia cuneifolia*, *Cameraria angustifolia*, *Caesalpinia anacantha*, and *Cephalocereus polygonus*. In addition the poisonous properties of *Comocladia dodonea*, *C. mollifolia*, *Metopium brownei*, *M. toxiferum*, *Jatropha hernandifolia* and *Hippomane spinosa* were well known, and these plants, too, had to be avoided.

Nowhere on the island did I see trees of fifty to eighty feet as mentioned in the coastal survey report of 1868. The tallest plants were specimens of *Haitiella ekmanii* which stood out in the profile of the forest canopy. These are the "thrinax-like plants" mentioned by Ostenfeld. The largest trees on the island were *Sarcomphalus dominensis*, *Coccoloba pubescens*, *C. diversifolia*, *Bursera simaruba*, and *Ficus populnea* var. *hispaniolae*. A

single specimen of *Clusia rosea*, also one of the more massive plants on Beata, was seen. Around these few conspicuous plants the vegetation consisted of a dense growth of smaller trees and shrubs, much branched and forming an intertwined canopy of branches six to ten feet above the ground. Many of these plants were microphyllous or had leathery shiny leaves. Broad-leaved plants such as *Ulbrichia beatensis* were few. *Comocladia dodonaei* and *C. mollifolia* appeared to be the most numerous. *Cordia buchii* and *Tabebuia ostenfeldii* in full flower presented the most color. The other common species were *Malpighia setosa* and *M. domingensis*, *Capparis flexuosa*, *Krugiodendron ferreum*, *Schoepfia obovata*, *Randia parvifolia*, *Exostemma caribaeum*, *Elaeodendron xylocarpum* (extremely variable in leaf size and shape), *Plumeria obtusa* (also extremely variable), *Securinega acidoton* and *S. neopeltandra*, *Amyris granulata*, *Isodorea leonardii*, *Trichilia cuneifolia*, *Reynosia cuneifolia*, *Samyda pubescens*, *Guettarda xanthocarpa* and *G. stenophylla*. *Opuntia moniliiformis* was the only cactus seen in the shrub thickets. Herbaceous growth was conspicuously lacking throughout the interior of the island. *Setaria setosa* was the only grass found in the woodland. *Euphorbia hepatica* and *Commelina diffusa* occurred on the rocks or in pockets of soil. *Zephyranthes bifolia*, a bulbous plant, occurred in small pockets. This plant was not in flower at the time I visited the island, but transplanted bulbs later flowered at Barahona and in the greenhouse in Cambridge. The absence of herbaceous growth was as conspicuous as the extensive development of vines. Much of the progress through the interior was possible only with the continuous stroking of a machete. *Galactia dictyophylla*, *Mesechites repens*, five species of *Cissus*, *Stegnosperma cubense*, *Paullinia jamaicensis*, *Aristolochia bilobata*, and *Chiococca alba* were rampant. Equally troublesome to the foot traveler was the accumulation of dried leaves on the ground. Apparently decay occurred very slowly, for the leaves were deep in many places, and as they hid not only the rough dogtooth surface of the limestone but also the small depressions and many crevices, progress had to be made cautiously.

Epiphytes in general were few in the thorn shrub area. *Tillandsias* were relatively abundant in a few places but generally scarce when compared with a comparable location elsewhere in Barahona province. Only two species of orchids were found, and these occurred only on the very low branches or the prostrate trunks, as described by Ostenfeld.

Six and a quarter miles to the south of Beata is the island called Alta Vela, occasionally spelled Alto Vela (FIG. 7). From a botanical point of view this island was less interesting than Beata, but historically Alta Vela is better known and has played an often forgotten role in American history.

Alta Vela Island was discovered by Columbus on August 20, 1494. As J. B. Thacher (*Christopher Columbus* 2: 336-7. 1903) describes the event, Columbus "anchored at a small island, or rather a rock which rises singly out of the sea opposite to the long cape stretching southward from the center of the island, to which promontory he gave the name of Cape Beata.

The rock at which he anchored had an appearance at a distance of a tall ship under sail and he called it Alta Vela. Several seamen were ordered to climb the rock to watch out for the two lost ships of his squadron. Descending from the summit the sailors killed on the island of Alta Vela eight sea wolves which were sleeping on the sands, knocked down many pigeons and other birds with sticks and took others with their hands; for in this unfrequented island the animals seemed to have none of the wildness and timidity which is produced by hostility of man."

As Alta Vela, like Beata, was destitute of natural water supplies, few ships stopped there except for food or firewood, and no evidence can be found in the literature that the island was ever occupied by other than transients. It is a small island about three quarters of a mile long and a half-mile wide composed originally of a "remarkable bell-shaped hill, the summit 500 feet above sea level." Alta Vela Island almost became a possession of the United States in the middle of the nineteenth century, and the dispute over the ownership of it forms an interesting part of American political history. The story is told in detail in the Senate Executive Document No. 38 of the second session of the Fortieth Congress (1868), in Document No. 17 of the third session of the Forty-first Congress (1871), and reviewed in "The United States and Santo Domingo 1798-1873," pages 287-337, by Charles C. Tansill. I am quoting liberally from these documents in summarizing the history of Alta Vela.

The United States Congress, on Aug. 18, 1856, passed a law to legalize claims of American citizens to unoccupied islands with guano deposits. The law stated, "When any American citizen chances to discover a deposit of guano on any island, rock or key not within the lawful jurisdiction of any other government and takes peaceful possession thereof, and occupies the same, such island, rock or key may, at the discretion of the President, be considered as appertaining to the United States." As soon as practicable the claimant should give notice to the Department of State of such discovery and occupation describing the island, rock or key and the latitude and longitude thereof as near as may be, and showing that such possession was taken in the name of the United States and should furnish satisfactory evidence to the State Department that such island was not at the time of discovery thereof or the taking possession of and occupation thereof by the claimant in the possession or occupation of any other government. After these conditions were met the discoverer might at the pleasure of Congress be allowed "exclusive rights of occupying such island, rocks or keys for the purpose of obtaining guano and of selling and delivering the same to citizens of the United States."

It was with this law in mind that a schooner owned by the Baltimore firm of Patterson and Murguiendo took possession of Alta Vela on Feb. 23, 1860. In May and June the Secretary of State and the State Department of Buchanan's administration were notified that a claim to the uninhabited and unclaimed island was made for the United States. Mining operations were carried on, and when a Dominican vessel stopped at the island in September of that year, its officers were given a sample of the guano. In

early October the Dominican government ordered the Americans to leave the island, which they refused to do, and on the twenty-third of October a vessel of the Dominican government landed troops who arrested the workers and removed the mining equipment. These workers and a company representative sent to obtain their release were held prisoners in Santo Domingo city for nearly thirty days, in spite of promises of safe conduct. The company protested the action to the American Secretary of State. Buchanan's term expired, Johnson became president, and Seward was appointed Secretary of State. Black, the former Secretary, was hired as counsel for the protesting firm. Seward at the time was negotiating with the Dominican government for the use of Samana Bay at the northeast corner of Hispaniola as a United States naval base and was not anxious to force the claim of the previous administration regarding Alta Vela. In fact Seward was thought to be guilty of duplicity when he informed a competing firm, Webster & Co. of New York, that in his opinion the territory under question belonged to the Dominican government. An intimate friend of Seward was found to have a large interest in Webster & Co., and the rage against Seward and Johnson increased when it was learned that the Dominican government had given permission to the Webster company to remove guano from Alta Vela. Patterson and Murguiendo Co., the original claimant to the Alta Vela guano, reported to the State Department that at the current rate of mining and exporting at two thousand tons per month, the guano would soon be exhausted. When the House of Representatives, a few months later on Feb. 24, 1868, agreed on a resolution of impeachment against Johnson, the events which had occurred in Seward's handling of the Alta Vela dispute ranked high. The House Committee on Foreign Affairs, which investigated the dispute, reported, "We are compelled to say that the case is too clear to allow of the least hesitation. Santo Domingo was guilty of an inexcusable outrage upon the rights of the memorialists and a gross insult to the United States." In May of 1869 an appeal was made to Hamilton Fish, the new secretary of state under Grant, for a decision in the case. Finally in May of 1870 Fish reported to the attorneys for Patterson and Murguiendo that all of the documents and pertinent correspondence had been placed before President Grant, who after due consideration determined that no sufficient reason appeared for reconsidering the conclusions heretofore reached.

With that decision Alta Vela dropped from the news. Apparently in due time the guano deposits were mined out. From information and estimates which appeared in the Senate Executive Documents, Alta Vela once contained fifteen thousand tons of guano. An analysis of this material showed it contained 29.16% phosphoric acid and 70.84% lime.

Apparently the mining operation forced the sea birds to change their habits, for no large numbers of them roost on Alta Vela today. The scars of the mining operations on the leeward slopes of the island are still visible, and artifacts of mining still litter portions of the hill (FIG. 10).

Alta Vela, with no wood, water, or fertile soil, remains a desolate outpost. Today a single house and a few small supply buildings take care of the

needs of a lighthouse keeper. The lighthouse at the summit of the hill represents one of the southernmost beacons of the Greater Antilles (FIG. 9).

For the botanist visiting Alta Vela today there is little of interest. The island is bounded by severe wave-washed and undercut cliffs (FIG. 8).

Around the island the bottom drops off sharply, and within a short distance of the shore it consists primarily of boulders offering poor if any anchorage in the heavy seas that continuously wash the island. Landing from the destroyer escort which provided transportation for me proved hazardous, and in fact the vessel stayed under power to hold its position during my visit to the island. Apparently previous occupants of the lighthouse keeper's position tried to grow vegetables and crops of cotton on the slopes on the leeward side. The current keeper informed me he had learned this to be futile, for the lack of sufficient moisture and the frequent dousings with salt spray killed off all his attempted crops.

Alta Vela today has primarily a weedy vegetation. The few woody plants which occurred on the island were located in ravines, primarily on the leeward side of the island (FIG. 10). Those shrubs struggling for existence on the crest of the hill or on the windward side were severely wind-blown and malformed (FIG. 9). These woody plants were few. *Capparis flexuosa* and *C. cynophallophora*, *Ficus populnea*, *Pithecellobium unguis-cati* and *Duranta repens* represented the largest woody plants. *Morinda royoc*, *Iresine angustifolia*, *Eupatorium corymbosum*, and *Sesbania sericea* were the most common plants of low stature. The coastal or flatland areas were dominated by weedy species. In fact the list of twenty species found on Alta Vela and not on Beata would show only pan-Caribbean, if not pan-tropical weeds. There are no evidences of even interesting species of limited range found on the island.

Many of the areas, particularly the mined-out areas on Alta Vela, appeared from the sea to be grassy meadows (FIG. 10.). These were deceptive even from nearer by. The grasses and sedges giving this impression, *Paspalum bakeri*, *P. adspersum*, *Setaria geniculata*, *Cyperus compressus*, *Fimbristylis spathacea*, formed dense stands one to three feet high. However, mixed in with these grasses and hidden by them were extensive mat-like growths of *Opuntia antillana*. *Opuntia dillenii* was common around the edges of these swales. On the exposed rocky outcrops at the sea-cliff margin of the island the vegetation is stunted and consists of the usual halophytes of such areas, *Lithophila muscoides*, *Portulaca oleracea*, *Talinum paniculatum*, *Iresine angustifolia*, and *Sesuvium portulacastrum*. Common in such locations, however, is the turk's cap cactus, *Cactus lemari*.

Alta Vela, by contrast to Beata, has a flora consisting entirely of a woody pauperous vegetation. Whether the island ever had the interesting flora found on Beata is impossible to speculate. Probably its environment was such that shelter was lacking, and only the most hardy of Caribbean plants could grow. Mining operations may have removed some of the vegetation from the sheltered leeward slopes, but the abundance of birds

necessary to produce the guano may also have played a role in the development of the present weedy vegetation.

The vegetation on Alta Vela offers little information regarding the affinities of the flora of the southern coast of Hispaniola, particularly when contrasted with that of Beata.

Beata Island possesses a flora consisting of 118 genera and 168 species, as based on the collection records of Ostenfeld and Howard. The vast majority of the species on Beata are wide-ranging species, but thirty-five of them, representing twenty per cent of the flora, are species of limited distribution and contribute information regarding the affinities of this islet. In addition, three good species are to be currently regarded as endemic to Beata. These are *Ulbricia beatensis*, *Tabebuia ostenfeldii*, and *Galactia dictyophylla*. One species, *Euphorbia hepatica*, is known elsewhere only from Navassa Island. *Guettarda xanthocarpa*, *G. stenophylla*, *Amyris granulata*, and the hybrid between *Coccoloba uvifera* and *C. pubescens* are known only from the vicinity of Trujin on the Barahona peninsula. *Salicornia bigelovii* has also been collected by Ekman on Gonave Island but is not known from the main island of Hispaniola. Two species, *Elaeodendron ehrenbergii* and *Antirrhoea elliptica*, have been previously collected only in the Cul de Sac, with the latter known only from Isla de Cabritos in Lake Enriquillo.

In general the relationship of the vegetation of Beata Island is with the dry-land shrub vegetation extending from southeastern Haiti through the Barahona peninsula into the Enriquillo valley and eastward to the vicinity of Azua. There is no indication in the Beata flora of affinities with the vegetation of the western end of the southern peninsula of Haiti, a floristically distinct area frequently pointed out by Ekman. Geologically, as well as botanically, Beata appears to be a fragment of recent fracture from the Barahona peninsula.

A comparison of Beata Island with the other islands intensively studied by Ekman reveals that for its small size and lack of topography Beata has indeed a very interesting vegetation. Beata ranks in size with Navassa (*Arkiv för Botanik* 22A (16): 1-12. 1929). The number of species found on Beata is greater, the percentage of endemics about equal; the percentage of introduced or weedy species is much less and the number of interesting species of limited range much higher. The larger size of Gonave Island and the greater range of topography, coupled with its location, have produced a much larger flora, 928 species, than that found on Beata (*Arkiv för Botanik* 23A (6): 1-73. 1930). The same is true of Tortue Island, which has 889 species (*Arkiv för Botanik* 22A (9): 1-61. 1929). Gonave, Tortue, and Navassa are reported to have a soil developed in all or parts of the islands. All seem to receive sufficient rainfall to support the diversified vegetation present. All are in the paths of prevailing winds and currents which would aid the introduction of additional species of plants from the mainland of Hispaniola. Beata stands by contrast. No accurate rainfall records are available for Beata. According to the naval personnel stationed on the island the rainfall is very slight. The catchments estab-

lished on the buildings on Beata do not provide sufficient rainfall for the personnel, and water must be imported. The accumulation of leaves on the surface of the plateau supports the conclusion that sufficient moisture is not available for decay of vegetation. Interestingly, termite action was not noticed on the island. The lack of soil on Beata has prevented the development of a fern flora or of extensive herbaceous growth. The location of Beata, south of the Barahona peninsula, has prevented the introduction of many species from the mainland of Hispaniola by natural transport. Particularly striking in the Beata flora was the complete lack of certain major groups of plants, such as the ferns, and the few examples of epiphytes and palms seen. Families and genera of flowering plants expected in similar dry thorn shrub areas of Hispaniola were also lacking. In particular the absence of members of the Piperaceae, Loranthaceae, Flacourtiaceae, Myrsinaceae, Sapotaceae, Labiatae, Solanaceae, Rutaceae, and Acanthaceae was noted. Characteristic genera such as *Pilea*, *Zanthoxylum*, *Trema*, *Phyllostylon*, *Maytenus*, *Casearia*, *Sideroxylon*, *Bumelia*, *Acacia*, and *Mimosa* were missing from the flora. Additional work on the flora of Beata may be expected to produce additional distributional records, but such work must be accompanied by an examination of the vegetation from Lago Trujin to Punta Beata for comparison. The succession of plant life in the abandoned salt pans should be followed for information on replacement of vegetation in dry-land areas. Nowhere could a study of the development of such a high percentage of toxic and spiny plants as related to the factors of their environment be better attempted.

A LIST OF PLANTS OF BEATA AND ALTA VELA ISLANDS

HYDROCHARITACEAE

Thalassia testudinum Koenig. Beata; *Ostenfeld s.n.*, Howard by observation.—A marine plant particularly common off the north shore in shallow water.

GRAMINEAE

Cenchrus brownii R. & S. Alta Vela; *Howard 12474*.

Cenchrus myosuroides H.B.K. Alta Vela; *Howard 12464*.—Found near the crest of the hill. The stems prostrate, to six feet long.

Cenchrus pauciflorus Benth. Beata; *Howard 12419*.—Plant of open sandy area at the northwest corner of the island. Stems prostrate, radiating.

Panicum adspernum Trin. Alta Vela; *Howard 12462*.—A prostrate plant with radiating branches.

Panicum maximum Jacq. Beata; *Ostenfeld by observation, Howard 12389*.—A common grass in areas around bays and old salt pans.

Paspalum bakeri Hackel. Alta Vela; *Howard 12480*.—A common clump grass, perhaps the most abundant and dominant plant on old

guano mined areas. Previously collected on Inagua, Cuba and Barbuda. This is the first record from Hispaniola.

Setaria geniculata (Lam.) Beauv. Alta Vela; *Howard 12471.*

Setaria setosa (Sw.) Beauv. Beata; *Howard 12493.* — Perhaps the only grass growing on limestone in brush thickets. Plants few, scattered.

Sporobolus domingensis (Trin.) Kunth. Beata; *Ostenfeld 330*, Howard by observation. A beach grass dominating sandy areas in the northeast corner of the island. Sterile in August.

Sporobolus pyramidatus (Lam.) Hitch. Alta Vela; *Howard 12460.* — A rare plant; only one specimen seen on the lee side of the island.

CYPERACEAE

Cyperus compressus L. Alta Vela; *Howard 12465.* — An uncommon sedge found on rocks near the lighthouse.

Cyperus nanus Willd. Beata; *Howard 12400.* A single specimen found on the limestone benches near the coast.

Cyperus planifolius L. C. Rich. Beata; *Howard 12447.* Alta Vela; *Howard 12467.* A clump-forming plant found on sand, especially in swales on Beata. On Alta Vela this species is more common, being found in large colonies on the leeward slopes where guano had been mined. This area has been burned frequently, and the charred bases of these plants give the hill a blackened appearance from the sea.

Fimbristylis spathacea Roth. Alta Vela; *Howard 12466.* — A sedge occurring from sea level to the crest of the island. More abundant at the lower elevations.

Mariscus bruneus (Sw.) Clarke. Beata; *Ostenfeld 318, 339.*

Remirea maritima Aubl. Beata; *Howard 12427.* — This unusual sedge was particularly common in the grassy areas in the northeast corner of Beata Island on sand at the edge of limestone. The white bracts cause the plant to be conspicuous even from a distance. The species has been reported previously only from the vicinity of Barahona on Hispaniola. One locality record is known from Puerto Rico. The species is more common in Trinidad, South America, and Africa.

BROMELIACEAE

Tillandsia balbisiana Schl. Beata; *Howard 12349.* — An epiphyte in the shrub thickets.

Tillandsia circinnata Schl. Beata; *Ostenfeld 327.*

Tillandsia recurvata L. Beata; *Howard 12508.* — A common epiphyte found only on the western side of the island on shrubs in the lee of the cliff face.

Tillandsia usneoides L. Beata; *Ostenfeld 315, Howard 12380.* An epiphyte of general occurrence.

Tillandsia utriculata L. Beata; *Howard* 12374. — The largest epiphyte found in the interior of the island.

COMMELINACEAE

Commelina diffusa Burm. f. Beata; *Howard* 12494. — A fleshy herb found on the limestone in the shrub area away from the coast.

PALMAE

Haitiella ekmanii (Burret) Bailey. Beata; *Howard* 12369, 12420. — Apparently the only palm on Beata Island. At the northern end of the island this species is quite abundant in windswept shrub formations, averaging here ten feet in height. Toward the southern end and in the interior in the shrub thickets the palm reached forty feet in height. This species was known previously only from the southern peninsula of Haiti at Anses-à-Pitre on Morne Savane Lafleur (Contrib. Gray Herb. 165: 5-9, 1947).

AMARYLLIDACEAE

Zephyranthes bifolia (Aubl.) Roem. Beata; *Howard* 12499-a. — A bulbous plant occurring in cracks and crevices in the limestone in the interior of Beata. The plant was in sterile condition in August when collected. The bulbs collected were planted and flowered in November in Barahona, while others flowered in March in Cambridge, Mass., allowing positive determination. The species is relatively common on limestone in Hispaniola but is not known elsewhere to me at such a low altitude.

ORCHIDACEAE

Laeliopsis domingensis Lindl. (*Broughtonia domingensis* Rolfe). Beata; *Ostenfeld s.n.*, *Howard* 12402, 12428. — An epiphyte of the shrub area, widespread on the island. Ostenfeld notes that these plants occur primarily on the lower branches or trunks of the shrubs. I can verify that this seems to be the pattern of occurrence of the species on the island.

Oncidium intermedium Bert. Beata; *Howard* 12518. — Locally abundant in the thorn shrub areas along the western coast of the island.

ULMACEAE

Celtis trinervia Lam. Beata; *Howard* 12372. — Trees of fifteen feet with green fruit. In the thorn shrub areas on limestone.

MORACEAE

Ficus populnea Willd. var. *hispaniolae* Urb. Beata; *Howard* 12516. Alta Vela; *Howard* 12482. — A twenty-foot tree on Beata Island occurring in the thorn shrub. The striking dark green foliage makes

this plant conspicuous in the thickets. On Alta Vela this species is generally found on the windswept eastern slopes, where plants from one to fifteen feet tall were seen.

URTICACEAE

Rousselia humilis (Sw.) Urb. Beata; *Howard 12375*. — One of the few terrestrial herbs in the limestone areas.

OLACACEAE

Schoepfia obovata Wr. Beata; *Howard 12383*. — An exceedingly common shrub of thorn thickets. Plants occur to eight feet tall.

ARISTOLOCHIACEAE

Aristolochia bilobata L. Beata; *Howard 12366*. — A sterile vine with distinctive foliage.

POLYGONACEAE

Coccoloba diversifolia Jacq. Beata; *Howard 12361*. — A common tree fifteen to twenty-five feet in height in thickets on limestone.

Coccoloba pubescens L. Beata; *Howard 12352*. — One of the largest trees on Beata Island reaching twenty-five feet in height. It occurs on the limestone from the benches of the west coast to the center of the island.

Coccoloba subcordata (DC.) Lind. Beata; *Howard 12488*. — Prostrate or ascending shrubs occurring on the limestone plateau.

Coccoloba uvifera L. Beata; *Howard 12489*. Alta Vela; *Howard 12453*. — Trees reaching fifteen feet are found along the coast in sandy areas.

Coccoloba uvifera \times **C. pubescens**. Beata; *Howard 12499*. — This new hybrid was first discovered south of El Caiman on Barahona peninsula, where several stands of the plant had developed between colonies of the parents. The hybrid is a true intermediate with the leaf shape of *C. uvifera* but the venation and texture of *C. pubescens*. The fruits were all sterile but of the size and shape of those of *C. uvifera*. Only a single specimen, eight feet tall, was found on Beata at the southern end of the sandy strip which occurs on the northwest corner of the island.

CHENOPODIACEAE

Atriplex pentandra (Jacq.) Standl. Beata; *Howard 12451*. — A single plant was found on the rocks of the coastal bench. Moscoso lists this plant without specific location in his catalogue of plants from the island. This is the first specimen of this species I have collected in Hispaniola.

Salicornia bigelovii Torr. Beata; *Howard 12442*. — A relatively abundant species mixed with *Batis* and *Sesuvium* along the lagoon

near the salt pans. Moscoso does not record this species from Hispaniola although Ekman collected it on Gonave Island near Trois Louis. Ekman reported the species was not found on the mainland, although it is found on the Atlantic coast of the United States and in Cuba. This collection represents the second record from Hispaniola, but again from an island, not the mainland.

AMARANTACEAE

Amaranthus gracilis Desf. Alta Vela; *Howard* 12458.—This species occurred as a weed in an old field on Alta Vela. Moscoso does not list it in his Catalogue, although I have now collected the taxon at Manzanilla and in the Enriquillo basin. Ekman found the same species on Gonave.

Celosia nitida Vahl. Beata; *Ostenfeld* 320.

Iresine angustifolia Euph. Alta Vela; *Howard* 12456.—The species occurs as a weed on the area disturbed by guano mining.

Lithophila muscoides Sw. Beata; *Ostenfeld* 345, *Howard* 12426. Alta Vela, *Howard* 12461.—On both Beata and Alta Vela this species was a prostrate plant of limestone coastal benches.

NYCTAGINACEAE

Boerhaavia caribaea Jacq. Beata; *Howard* 12487. Alta Vela; *Howard* 12472.—A sporadic weed occurring primarily in the grassy areas.

Neea subcoccinea Heimerl. Beata; *Howard* 12379.—Characteristic shrub of limestone plateau. Plants to eight feet tall with widespread branches. This species is apparently endemic to Barahona province and has been recorded previously only from that vicinity.

BATIDACEAE

Batis maritima L. Beata; *Howard* by observation.—A common woody perennial along the lagoon and edges of the salt pans on Beata.

PHYTOLACCACEAE

Rivina humilis L. Alta Vela; *Howard* 12476.—Plants to two feet tall were relatively common in the sheltered areas on Alta Vela.

Stegnosperma cubense A. Rich. (*Stegnosperma halimifolium* auct.). Beata; *Ostenfeld* 319, *Howard* 12507.—A trailing or scrambling fleshy-stemmed to woody bush quite common at the edge of the sand and limestone on the western coast of Beata Island. Moscoso does not give a specific location for the occurrence of this species in Hispaniola. D. J. Rogers (Ann. Mo. Bot. Gard. 36: 475. 1949) cites two collections by *Fairchild*, numbers 2605 and 2606, from Beata Island. He likewise records collections by Ekman from Massif des Cahos, Barahona, and Sierra de Ocoa.

AIZOACEAE

Sesuvium portulacastrum L. Beata; Ostenfeld and Howard by observation. — A common fleshy herb on sandy areas and occasionally on the limestone coastal benches.

PORTULACACEAE

Portulaca oleracea L. Beata; Ostenfeld 344, Howard 12450. — A common weed around the buildings in the northwest corner of Beata.

Portulaca phaeosperma Urb. Beata; Ostenfeld 346, Howard 12405. — A fleshy herb of sand and of limestone coastal benches.

Talinum paniculatum (Jacq.) Gaertn. Alta Vela; Howard 12477. — A stout herb of hillsides on both windward and leeward sides.

ANNONACEAE

Annona bicolor Urb. Beata; Howard 12356. — A shrub of the limestone plateau. Plants to fifteen feet tall with attractive reddish purple flowers. This species had previously been reported only from the vicinity of Barahona.

LAURACEAE

Cassytha americana Nees. Beata; Howard 12417. — An orange-colored parasitic vine on shrubs of the coastal limestone benches.

CRUCIFERAE

Cakile lanceolata (Willd.) Schulz. Beata; Howard 12444. — A fleshy herb of sandy areas at the northwest corner of Beata.

CAPPARIDACEAE

Capparis cynophallophora L. Beata; Ostenfeld 309, Howard 12406. Alta Vela; Howard 12485. — This species occurs in the shrub area on the limestone plateau on Beata. It is also the largest and most common tree on the leeward slopes of Alta Vela.

Capparis flexuosa L. Beata; Ostenfeld 317, Howard 12504, 12393. Alta Vela; Howard 12483. — A common scrambling shrub of the thickets of Beata and on the leeward slopes of Alta Vela.

LEGUMINOSAE

Caesalpinia anacantha Urb. Beata; Howard 12432. — One of the common shrubs in the windswept area on limestone at the northern end of Beata. Ekman found this species on Gonave Island and it has been collected at Montagnes du Trou d'Eau in Morne a Cabrits.

Caesalpinia ciliata (Berg.) Urb. Beata; Ostenfeld 325. — Previously recorded from Haiti only.

Caesalpinia glandulosa Bert. Beata; *Howard* 12435.—A spreading shrub to five feet tall in the windswept shrub area on limestone at the northern end of Beata. Moscoso reports that this species was collected by Bertero in the Dominican Republic, but the location is unknown.

Canavalia maritima (Aubl.) Thou. Beata; *Howard* 12392.—A common beach vine on sandy areas of Beata.

Cassia buchii Urb. Beata; *Ostenfeld* 313, *Howard* 12448.—This low shrub was found only on limestone. Urban, in determining the plants collected by Ostenfeld, felt that the Beata plants represented a distinct form. I feel this is an ecological variant due to the habitat.

Cassia strigillosa Benth. Beata; *Howard* 12399.—A woody herb of the sandy areas.

Desmanthus virgatus (L.) Willd. Beata; *Howard* 12433.—A woody herb becoming five feet tall. In thicket and windswept areas of the plateau.

Desmodium triflorum DC. Alta Vela; *Howard* 12475.—A prostrate herb occurring on rocks at the summit of the island.

Galactia dictyophylla Urb. Beata; *Ostenfeld* 329, 332, *Howard* 12500.—This relatively common vine occurs on the limestone cliff faces. The species is endemic to Beata Island.

Indigofera suffruticosa Mill. Beata; *Howard* 12398.—A weedy herb of sandy areas, growing to four feet in height.

Pithecellobium unguis-cati (L.) Benth. Alta Vela; *Howard* 12455.—A low shrub on the windward slopes of Alta Vela.

Sesbania sericea (Willd.) DC. Alta Vela; *Howard* 12457.—A shrub of three feet on the leeward slopes of the island.

Tephrosia cinerea (L.) Pers. Beata; *Howard* 12423.—A common woody herb of sandy beaches.

One of the common small trees of Beata Island remains unidentified (*Howard* 12384). This fifteen-foot tree was not in flower or fruit during my visit there. The leaves are evenly pinnate and consist of four to six leaflets. The leaflets are orbicular-rhombic in outline with the midrib placed off the median. The texture of the leaflets is coriaceous and when dry both surfaces are densely reticulate. In appearance the specimens collected resemble *Pithecellobium*, but until fertile material is available the plant remains unidentified.

ERYTHROXYLACEAE

Erythroxylon areolatum L. Beata; *Ostenfeld* 308, *Howard* 12360.—A ten-foot spreading shrub relatively common in limestone plateau thickets.

ZYGOPHYLLACEAE

Guaiacum sanctum L. Beata; *Ostenfeld 304, 305, Howard 12502.* —
Trees of twenty feet in thickness on limestone.

Tribulus cistoides L. Beata; *Ostenfeld 326.*

RUTACEAE

Amyris elemifera L. Beata; *Howard 12401.* — A shrub of twelve feet occurring on the limestone plateau.

Amyris granulata Urb. Beata; *Howard 12344.* — A relatively common shrub of twelve feet occurring on the limestone at all elevations. The species was sterile in August. The type, from Trujin, was collected by Abbott.

SIMARUBACEAE

Picrodendron macrocarpum (A. Rich.) Britton. Beata; *Ostenfeld 293, Howard 12430.* — A common tree around the old salt pans. Plants reaching fifteen feet with spreading branches.

Suriana maritima L. Beata; Howard, by observation. — A common shrub of the sandy beaches on the west coast.

BURSERACEAE

Bursera simaruba (L.) Sarg. Beata; *Ostenfeld 253, 322, Howard 12515.* — Due to its colored bark, this is the most conspicuous tree in the open thorn thickets on limestone.

MELIACEAE

Trichilia cuneifolia (L.) Urb. Beata; *Howard 12388.* — A shrub of twelve feet occurring on limestone. Previously reported from Azua to Barahona on Hispaniola.

MALPIGHIACEAE

Malpighia domingensis Small. Beata; *Howard 12346.*

Malpighia setosa Spreng. Beata; *Howard 12501.*

Stigmaphyllo lингulatum (Poir.) Small var. *sericans* Ndz. Beata; *Ostenfeld 335*, Howard by observation.

EUPHORBIACEAE

Croton lucidus L. Beata; *Howard 12440.* — A four-foot shrub common along the edges of the old salt pans.

Croton polytomus Urb. Beata; *Howard 12407.* — Previously reported from Cadets on the northern peninsula of Haiti and considered endemic there. This was a common seven-foot shrub in the thickets.

Euphorbia buxifolia Lam. Beata; *Howard 12445.* — An herb of sandy and grassy areas and less frequent on limestone benches.

Euphorbia hepatica Urb. Beata; *Howard* 12425.—A prostrate plant growing in small holes in the limestone. This species was based on material collected by Ekman on Navassa Island. This is the second collection recorded for this insular endemic.

Gymnanthes lucida Sw. Beata; *Howard* 12505.—A common shrub in thickets, to eight feet tall.

Hippomane manchinella L. Beata; *Howard* by observation.—Common in restricted areas of coastal sand.

Hippomane spinosa L. Beata; *Howard* 12385.—A shrub of eight feet to a tree of twenty feet. Common in thickets and thorn shrub on the plateau. This species has been previously collected in Haiti. The toxicity of the sap of this plant far exceeds any of the other dermatitis-producing plants that I have encountered in the Antilles. After collecting specimens from one of the plants seen on Beata, I accidentally ran the sharpened branch through the shoulder of my shirt, without breaking the skin. A few hours later my shoulder became painful, and I discovered that a large blister was developing. Liquid continued to accumulate, forming several blisters, and the largest, by the time it broke, was fully two inches in diameter and an inch high. The amount of liquid that accumulated in the four large blisters produced was copious. A light compress was required for several days to protect the affected area, but no unusual soreness or after-effect was experienced. The sailors who are stationed at Beata Island confirmed the unusual blistering properties of this species and recognized them as being far more severe than those of *Hippomane manchinella*.

Jatropha hernandifolia Vent. Beata; *Howard* 12351.—A common weak-structured shrub to eight feet tall. The flowers are white and the mature fruit bright green.

Jatropha multifida L. Beata; *Howard* 12376.—It is difficult to believe that this plant, which occurs occasionally in thorn shrub areas of Barahona peninsula and in the plateau area of Beata, is not a native of the region.

Securinega acidoton (L.) Fawc. & Rend. Beata; *Howard* 12503.—One of the common very spiny shrubs of the thorn shrub thickets on the plateau.

Securinega neopeltandra (Griseb.) Urb. (*Chascotheca domingensis* Urb.). Beata; *Howard* 12358. Alta Vela; *Howard* 12481.—A common low shrub on both Beata and Alta Vela, which was collected in fruit in August.

ANACARDIACEAE

Comocladia dodonaea (L.) Urb. Beata; *Ostenfeld* 331, *Howard* 12514.

Comocladia mollifolia Ekm. & Helw. Beata; *Howard* 12517.—Barkley, who has studied my collections of *Comocladia*, refers this material to

C. mollifolia, which is based on an Ekman collection from Las Villas province in Cuba. I have previously collected this species from the vicinity of Pedernales. Together these two species of *Comocladia*, represented by spindly shrubs with a characteristic crown of pinnate leaves, represent the most abundant plants in most areas of the limestone plateau.

Metopium brownei (Jacq.) Urb. Beata; *Ostenfeld* 252, 321, *Howard* 12519.

Metopium toxiferum (L.) Krug & Urb. Beata; Howard by observation.— Both species of *Metopium* were observed growing to the rear of the sandy beach areas on the west coast. Both were present, but less abundant, on the limestone plateau.

CELASTRACEAE

Elaeodendron ehrenbergii Urb. Beata; *Ostenfeld* 251, 298, 299, 301, *Howard* 12396.— One of the most common plants in the more fertile sheltered areas back of the sand and coastal benches on the west coast. The plants averaged fifteen feet in height and were colorful with the abundant yellowish fruits.

Elaeodendron xylocarpum (Vent.) DC. Beata; *Howard* 12490.— A six-foot shrub on the limestone plateau. Previously known only from the vicinity of Barahona in Hispaniola but of widespread occurrence in the Antilles.

Maytenus reynosoides Urb. Beata; *Fairchild* 2613.— A microphyllous shrub apparently on the limestone.

Rhacomia crossopetalum L. Beata; *Howard* 12434.— A common shrub on limestone, to seven feet tall.

Schaefferia frutescens Jacq. Beata; *Howard* 12373.— A common shrub to ten feet tall, with red fruit.

SAPINDACEAE

Cardiospermum corindum L. Alta Vela; *Howard* 12486.— A weedy plant on open hillsides.

Paullinia jamaicensis Macf. Beata; *Howard* 12363.— An abundant but localized vine on the plateau. This appears to be the first record of the species from Hispaniola. It has been recorded previously from Jamaica and Cuba.

Sapindus saponaria L. Beata; *Ostenfeld* 307, *Howard* 12397.— A coastal tree of sandy beach areas, to twenty feet tall.

RHAMNACEAE

Colubrina ferruginea Brong. Beata; *Howard* 12390.— A coastal shrub often found with *Rhizophora* and *Thespesia* at the north end of Beata.

Colubrina reclinata (L'Her.) Brong. Beata; *Howard* 12496. — A common low shrub of sandy areas along the west coast.

Krugiodendron ferreum (Vahl.) Urb. Beata; *Howard* 12342. — A fifteen-foot shrub on the limestone plateau area.

Reynosia cuneifolia Urb. & Ekm. Beata; *Howard* 12353. — Abundant in thorn shrub on cliff faces and on the plateau.

Sarcomphalus domingensis (Spreng.) Krug & Urb. Beata; *Ostenfeld* 320, *Howard* 12348. Generally a small tree averaging fifteen feet, but with a few very old and large specimens in the dense thickets on the plateau. One of the largest trees on Beata.

VITACEAE

Cissus caustica Tussac. Beata; *Howard* 12341.

Cissus fuertesii Urb. Beata; *Howard* 12359.

Cissus macilenta (Planch.) Urb. Beata; *Ostenfeld* 336.

Cissus micrantha Poir. Beata; *Howard* 12362.

Cissus trifoliata L. Beata; *Ostenfeld* 311, *Howard* 12513. — These species of *Cissus* were equally abundant all over the island. In many places a single species or combination of them made penetration through the thorn shrub a matter of cutting one's way with a machete.

TILIACEAE

Corchorus hirsutus L. Beata; *Howard* 12404. — A shrub of sandy areas, to four feet high.

MALVACEAE

Gossypium hirsutum L. var. *punctatum* (Schum.) Hutch. Beata; *Ostenfeld* 324, *Howard* 12438. — A few scattered plants on the northwest corner of Beata led Ostenfeld to conclude that agriculture had been conducted there. Around the salt ponds and in the thorn shrub on the eastern coast of the island these plants are even more abundant, without accompanying evidences of cultivation.

Sida acuta Burm. Alta Vela; *Howard* 12470. — Woody herb around the lighthouse.

Thespesia populnea (L.) Soland. Beata; *Howard* 12410. — Low to almost prostrate coastal tree near the mangroves.

Ulbrichia beatensis Urb. (*Armouria beata* Lewton). Beata; *Ostenfeld* 312, *Howard* 12371. — This species was originally described by Urban from the Ostenfeld collection. The plant was again collected by D. Fairchild and P. H. Dorsett, members of the Allison V. Armour expedition, in 1932 and described by Lewton as a new genus. Both Howard (Bull. Torr. Club 76: 89–100. 1949) and Kearney (Amer. Midl. Nat. 46: 111. 1951) have discussed this genus. The collection I made in August was sterile, but the species is easily recognized.

STERCULIACEAE

Melochia tomentosa L. Beata; *Howard 12498*. — A common three-foot shrub on limestone, especially in the windswept northern area.

Waltheria americana L. Beata; *Ostenfeld 314*.

GUTTIFERAE

Clusia rosea Jacq. Beata; *Ostenfeld 296, Howard 12364*. — A single specimen, a tree of twenty feet, was found on the plateau area.

CANELLACEAE

Canella alba Murr. Beata; *Howard 12436*. — One of the largest trees in the thorn shrub around the salt pans. Plants to fifteen feet tall.

FLACOURTIACEAE

Samyda pubescens L. Beata; *Howard 12365*. — A low shrub of six feet on the limestone. A very attractive shrub when in full flower.

TURNERACEAE

Turnera ulmifolia L. Alta Vela; *Howard 12469*. — A common woody herb with brilliant yellow flowers. Abundant in disturbed areas.

PASSIFLORACEAE

Passiflora suberosa L. Beata; *Howard 12449*. — A fleshy vine on sandy areas and coastal benches.

CACTACEAE

Cactus lemari (Monv.) Brit. & Rose (*Melocactus*). Alta Vela; *Howard 12459*. — An extremely abundant turk's head cactus found on the exposed windward slopes and the south end of Alta Vela. Fruit a characteristic bright pink color.

Cephalocereus polygonus (Lam.) Brit. & Rose. Beata; *Howard 12492*. — A strict or candelabra-branched cactus reaching twenty feet in height. Abundant in open area on the limestone. The fruit is a bright red color.

Opuntia antillana Brit. & Rose. Beata; *Howard 12408*. Alta Vela; *Howard 12468*. — The most common low pad-type cactus on both Beata and Alta Vela. In the guano mined areas of Alta Vela this cactus is extremely abundant, although completely hidden by stands of grass and sedge. It is this cactus that makes progress through the "grassy areas" of both islands treacherous. It was observed that the stem segments of *Opuntia antillana* detach and attach themselves to trousers much more readily than those of *O. dillenii*.

Opuntia caribaea Brit. & Rose. Beata; Howard by observation. — This cactus with cylindrical joints was common in many areas of the thorn shrub on the limestone in the shrub thickets of Beata. This is the nastiest of all the cacti in Hispaniola, as the joints detach very readily, and any movement of the plant literally jettisons the spiny segments in all directions.

Opuntia dillenii (Ker.-Gawl.) Haw. Beata and Alta Vela; Howard by observation. — This plant is restricted to coastal areas and to areas of former human occupation.

Opuntia moniliformis (L.) Haw. Beata; Howard 12387. — An extremely common tree-type cactus found in the shrub thickets on the limestone plateau. The trunk of this cactus may be six inches in diameter and is covered with spines two to four inches long. The first branch may occur four to six feet from the ground. The flattened branches develop in all directions, and a thick stand of these plants is almost impossible to penetrate. The small flowers are attractive with the outer perianth parts red and the inner bright orange.

RHIZOPHORACEAE

Rhizophora mangle L. Beata; Howard 12414. — A coastal shrub most abundant on the north coast.

COMBRETACEAE

Conocarpus erecta L. Beata; Ostenfeld 316, Howard 12340. — A coastal plant on mud and marl flats. Trees to fifteen feet tall.

Conocarpus erecta L. var. *sericea* Griseb. Beata; Howard 12413. — Locally abundant at the northern end of Beata. Foliage heavily silky pubescent. Plants to ten feet tall.

Laguncularia racemosa (L.) Gaertn. Beata; Howard 12431. — Relatively abundant at the edges of the salt pans on the east coast of Beata.

MYRTACEAE

Cryptorhiza haitiensis Urb. Beata; Ekman (August Frett 7063), Howard 12345, 12446. — This species was described by Urban, based on material collected between Cueva Alta and Trujin and Juan Lopez and Trujin on the Barahona peninsula. Reference is also given in the original publication to a collection made by August Frett on Beata Island. I have been unable to learn anything further about the latter man or the nature or amount of collections he made on Beata. *Cryptorhiza haitiensis* is a common three-foot shrub growing on limestone on Beata Island. All plants were sterile in August. However, the distinctive foliage and aroma of the plant, coupled with the common names of cañelito and cañelillo, allowed determination of the collections. This plant was well known to all the sailors who were my companions. A strong aromatic tea made from the leaves

was recommended for upset stomachs or intestinal disorders; however, the same leaves were brewed into a mild and sweetened tea which we all drank with considerable pleasure nearly every evening aboard the boat.

Eugenia aeruginea DC. Beata; *Ostenfeld* 300.

Eugenia buxifolia (Sw.) Willd. Beata; *Ostenfeld* 300, 302, *Howard* 12347. — A common shrub of twelve feet on the limestone plateau.

Eugenia aff. fragrans (Sw.) Willd. Beata; *Howard* 12354, 12343. — An eight- to twelve-foot shrub collected on the marshy ground around the salt pans and on the limestone plateau. Records of this species from Hispaniola are all for higher altitude locations than these from Beata Island.

Eugenia linearis L. C. Rich. Beata; *Ostenfeld* 340, *Howard* 12381. — A fifteen-foot shrub found on the limestone plateau. This species was very common in restricted locations, with many seedlings and saplings in the vicinity. Urban regarded the Ostenfeld collection as a narrow-leaved form of the species, but the variation of leaf width with the age of the plant was striking in one colony in the field.

Eugenia rhombea (Berg.) Krug & Urb. Beata; *Howard* 12350. — A common shrub, generally about eight feet tall. It occurred on the limestone, but was most abundant in sheltered areas along the western coast of the island.

THEOPHRASTACEAE

Jacquinia barbasco (Loefl.) Mez. Beata; *Howard* 12409. — Bushes of five feet with abundant red fruits were found along the north coast of the island.

Jacquinia linearis Jacq. Beata; *Howard* 12441. — A small bush two to three feet tall was found in the windswept area along the north coast of the island. This species has not previously been reported from the southern coast of Hispaniola.

APOCYNACEAE

Cameraria angustifolia L. Beata; *Howard* 12403. — This species was illustrated by Burman in *Planteae Americanae* in describing Plumier's plants and was described by Linnaeus (Sp. Pl. 210. 1753). Moscoso reports this species was collected by Robert Schomburgk (no. 145), but no location was given for the collection. In 1926 Urban described a new species, *Cameraria linearifolia* (Ark. Bot. 20A (5): 39. 1926), based on an Ekman collection, which Woodson later reduced to synonymy under *C. angustifolia* (N. Am. Fl. 29: 121. 1938). Ekman's material came from Morne Cadets in Haiti. To the best of my knowledge neither Plumier nor Schomburgk was on Beata Island, and so this species may well be expected in the Barahona province.

probably in the Enriquillo valley and possibly in the limestone areas south of Trujin.

The material I collected on Beata Island in August came from a twenty-foot tree. Plants were relatively common in local areas along the cliff on the west coast. The trees were in flower and fruit. A description of the mature fruits has been lacking in the literature. The samara-type fruits were paired, each samara being 22-24 mm. long. The lateral wings, located slightly above the median line of the fruit, are strongly veined. The apex of the samara is emarginate when mature and deeply emarginate-cleft in development. The wings are lobed about one third from the base. The lobes are rounded above and cuneate at the base of the fruit. At the broadest part of the wings the fruit is 11 mm. wide.

Echites umbellata Jacq. Beata; *Howard* 12506.—A woody vine becoming shrubby. The attractive white flowers make this a conspicuous plant on the sandy beaches.

Lochnera rosea (L.) Rchb. Beata; *Howard* by observation.—An introduced ornamental planted near the buildings in the northwest corner of Beata.

Mesechites repens (Jacq.) Miers. Beata; *Ostenfeld* 334, *Howard* 12510.—A very common vine just back of the sandy beaches and in certain areas of the limestone.

Plumeria obtusa L. (*P. beatensis* Urb., *P. ostenfeldii* Urb.). Beata; *Ostenfeld* 249, 341, *Howard* 12424, 12491.—A common shrub of the limestone area most abundant in the windswept northern end. The number of specimens representing the two collections I made show sufficient variation to support Woodson's reduction of the Urban species (N. Am. Fl. 29: 117. 1938).

CONVOLVULACEAE

Calonyction tuba (Schlecht.) Colla. Beata; *Ostenfeld* 323, *Howard* 12394.

Evolvulus alsinoides L. var. *grisebachianus* Meisn. Beata; *Howard* 12395.—Herbaceous plants of sandy beaches, especially on the west coast.

Ipomoea acuminata (Vahl.) R. & S. Beata; *Ostenfeld* 333.

Ipomoea eriosperma (Desr.) Urb. Beata; *Ostenfeld* 343.

Ipomoea pes-caprae (L.) Sweet. Beata; *Howard* by observation.

Ipomoea tiliacea (Willd.) Choisy. Alta Vela; *Howard* 12463.

Jacquemontia jamaicensis (Jacq.) Hall. Beata; *Howard* 12437.—An abundant vine in thorn shrub on limestone.

BORAGINACEAE

Cordia buchii Urb. Beata; *Howard* 12511, 12495.—A very attractive shrub of twelve feet with red-orange flowers and yellowish fruits

turning orange. Common on the limestone and occurring on the faces of the cliffs.

Bourreria maritima O. E. Schulz. Beata; *Howard* 12378. — An eight-foot shrub of limestone areas, previously reported only from Cabo Falso and considered a dry-land coastal endemic of Barahona province.

VERBENACEAE

Avicennia nitida Jacq. Beata; *Howard* 12412. — A coastal plant of twelve feet. Most abundant on the north coast.

Citharexylum fruticosum L. Beata; *Howard* 12377. — A shrub of ten feet in height in the thorn shrub.

Clerodendron spinosum (L.) Spreng. Beata; *Howard* 12415. — A low shrub of two feet which seems to occur only in the larger pits in the limestone plateau.

Duranta repens L. Alta Vela; *Howard* 12484. — A common shrub to eight feet in height occurring only on the leeward side of the island.

Lantana reticulata Pers. Beata; *Howard* 12391. — A shrub of three feet occurring on sandy areas.

Stachytarpheta jamaicensis (L.) Vahl. Beata; *Howard* 12411. Alta Vela; *Howard* 12473. A weedy herb of sandy areas near the buildings and the salt pans.

BIGNONIACEAE

Tabebuia ostenfeldii Urb. Beata; *Ostenfeld* 342, *Howard* 12509, 12497. — A shrub five to six feet tall growing on limestone and especially on the cliff faces. The small grayish foliage coupled with the pale lavender flowers makes this an attractive plant and a rather distinct species. The species is based on the Ostenfeld collection but has also been collected by Ekman on Gonave Island and recorded by him from Anses-à-Pitre on the Barahona peninsula.

RUBIACEAE

Antirrhoea lucida (Sw.) Hook. Beata; *Howard* 12382. — An attractive fifteen-foot tree on limestone.

Antirrhoea elliptica Urb. & Ekman. Beata; *Howard* 12418. A low two-foot shrub occurring abundantly in the low windswept formation at the north end of Beata Island. This species was described from material collected by Ekman on Cabritos Island in Lake Enriquillo. It has not been reported from the Barahona peninsula, and this represents the second record of its occurrence.

Chiococca alba (L.) Hitchc. Beata; *Howard* 12367. Alta Vela; *Howard* 12479. — A common, often stout vine in open thorn shrub throughout the island of Beata. On Alta Vela the species forms a rampant shrub on the lee hillsides.

***Ernodea littoralis* Sw.** Beata; *Howard 12429.*

***Exostemma caribaeum* (Jacq.) R. & S.** Beata; *Howard 12386.* — A fifteen-foot tree in the thorn shrub on the limestone plateau.

***Erithalis vaccinifolia* (Griseb.) Wr.** Beata; *Howard 12416.* — A prostrate woody shrub occurring in large sink areas in the windswept formation at the northern end of Beata Island. The white flowers and shining black fruits make this a particularly attractive plant. This species has previously been known from Cuba. While Standley (N. Am. Fl. 32: 280. 1934) cites Santo Domingo as the known distribution of the species it is not listed by Moscoso, and I have seen no material from this island.

***Guettarda stenophylla* Urb.** Beata; *Howard 12512.* — A five-foot shrub growing on the cliff faces on the western side of Beata Island. Only one previous collection from El Charco del Gato on the Barahona peninsula is known to me.

***Guettarda xanthocarpa* Britton.** Beata; *Howard 12368.* — A fifteen-foot tree in the thorn shrub on the limestone plateau. This species has been collected in several locations on southern Barahona peninsula. Standley refers this species to the synonymy of *G. cueroensis* Britton N. Am. Fl. 32: 236. 1934), but a field knowledge of both species prompts me to retain *G. xanthocarpa*, as it occurs in Hispaniola, as distinct.

***Isidorea leonardii* Urban.** Beata; *Howard 12357.* — A five-foot shrub on the limestone plateau.

***Morinda royoc* L.** Beata; *Howard 12439.* Alta Vela; *Howard 12454.*

***Psychotria nutans* Sw.** Beata; *Howard 12355.* — A six-foot shrub in thorn shrub on limestone plateau.

***Randia parvifolia* Lam.** Beata; *Howard 12370.* — This eight-foot shrub occurred in the thorn shrub on the limestone plateau.

***Strumpfia maritima* Jacq.** Beata; *Howard 12421.* — A common low shrub in the windswept area at the northern end of Beata Island.

COMPOSITAE

***Borrichia arborescens* (L.) DC.** Beata; *Ostenfeld 337, Howard 12422.* — A low shrub occurring at the dried edges of the mangrove swamps.

***Eupatorium corymbosum* Aubl.** Alta Vela; *Howard 12478.* — A very abundant shrub on all areas of Alta Vela.

***Tetranthus cupulatus* Urb.** Beata; *Howard 12443, 12452.* — Previously reported from Paradise on the Barahona peninsula. A white-flowered herb in holes in coastal limestone benches.

EXPLANATION OF PLATES

PLATE I

FIG. 1. Beata Island as seen from the west, midway of its length.

FIG. 2. Sandy beach on the west coast of Beata Island looking to the south. *Ipomoea pes-caprae* is the vine at the edge of the sand. *Coccoloba uvifera* and *Suriana maritima* form the first shrub zone. The major cliff profile is at the right.

PLATE II

FIG. 3. Grass-covered wind-blown sand zone encroaches on the limestone at the north end of Beata Island.

FIG. 4. A shrub zone on the deeply fissured limestone at the north end of Beata Island. Most of the shrubs in the foreground are rooted in crevices. Palms in the background are *Haitiella ekmanii*.

PLATE III

FIG. 5. Thorn shrub vegetation on the plateau area of Beata Island. The large tree at the left is *Bursera simaruba*.

FIG. 6. A group of tree cacti, *Opuntia moniliformis*, on the plateau limestone of Beata Island.

PLATE IV

FIG. 7. Alta Vela Island as seen from the north in the pass from Beata Island.

FIG. 8. The typical precipitous shore line of Alta Vela Island. A man in the upper right corner is in an area of turks head cactus, *Cactus lemari*.

PLATE V

FIG. 9. The light-house tower at the crest of Alta Vela. The wind-swept shrub occurs on limestone boulders.

FIG. 10. The southeast corner of Alta Vela showing the scars of the early guano-mining operations still visible. Shrubs in the lee of the hill at the right are *Capparis cynophallophora*. The grassy area near the shore line hides large stands of *Opuntia antillana*. The destroyer escort vessel "27 de Febrero" stands by off shore.



HOWARD, VEGETATION OF BEATA AND ALTA VELA



HOWARD, VEGETATION OF BEATA AND ALTA VELA



HOWARD, VEGETATION OF BEATA AND ALTA VELA



HOWARD, VEGETATION OF BEATA AND ALTA VELA



HOWARD, VEGETATION OF BEATA AND ALTA VELA

ON THE PRIMARY VASCULAR SYSTEM AND THE NODAL ANATOMY OF EPHEDRA

MARGERY P. F. MARSDEN AND TAYLOR A. STEEVES *

With three plates

THE AFFINITIES of the Gnetales have long been a subject of debate among students of Pteropsid relationships, particularly in regard to possible associations with the Coniferales and with the Dicotyledons. In this type of study the primary vascular anatomy usually figures prominently. *Ephedra* is often referred to as having a two-trace system of foliar vasculature. Marsden and Bailey (1955) recently suggested that the two-trace unilacunar node is a basic pattern in Pteropsida, and they described *Ephedra* as having a eustelic primary vascular system with two traces supplying each leaf from a single gap at the node, and attaching to separate portions of the eustele.

Nägeli (1858) first observed this vascular pattern in *Ephedra*. In subsequent literature, however, there is by no means general agreement about the primary vascular pattern in this genus. Thompson (1912) for example has stressed the importance of a girdle of nodal wood to the extent that he does not consider the internodal bundles to be directly related to the leaf traces, maintaining that the traces arise from this girdle and pass directly out into the leaves at the same node. He has also figured *Ephedra distachya* and *E. altissima* as distinctly bilacunar. Moreover, Strasburger (1872, p. 77) and Graham (1908-9), who are in general agreement with the eustelic pattern described by Nägeli, have reported in certain species an additional bundle between each pair of leaf traces in the internode below their insertion. Graham (1908-9) has further stated that this "complementary" or "accessory" bundle provides additional traces for the axillary bud. His descriptions of bundle fusions in the stem, moreover, do not agree with Nägeli's observations. Thompson (1912) has also reported complementary bundles, but regards them, like the other internodal bundles, as having their origin in the nodal girdle. Monoyer (1937) has,

* The authors are deeply grateful to Professor I. W. Bailey who originally suggested this problem. His guidance, advice, and interest throughout the course of this investigation have been an immense inspiration.

We wish to thank Dr. Adriance S. Foster who generously supplied material of several species of *Ephedra* from the University of California Botanical Gardens. Dr. Thomas W. Whitaker very kindly sent material several times during the course of this study, from the collection at the United States Department of Agriculture Station, La Jolla, California. The authors are indebted to Mr. Robert L. Dressler for assistance in the determination of specimens, and to Messrs. W. Barclay Ray and Ronald Shreve for aid in the collection of material. We are grateful to Mr. Peter M. Ray who gave generously of his time to assist with the preparation of the text and photographs.

in addition, reported that *E. fragilis* has three traces in each leaf, and these extend for one internode below their insertion, before anastomosing with certain sympodial bundles, the nature of which is not clear.

These conflicting views seemed to warrant a re-investigation of the primary vascular anatomy of this genus. This paper reports the result of a study of nine species of *Ephedra* with a view to determining the course of the primary leaf traces, their vertical extent in the stem, and their mode of departure from the stele, particularly in relation to the nodal girdle.

Ephedra is characterized by a marked xerophilous habit, with the leaves reduced to scales, and the young stems photosynthetic (PLATE I: 1). The epidermis is heavily cutinized, the stomata are sunken and the cortex has a mesophyll-like appearance (Plate I: 2, 3, 4). In some species the leaves are opposite and decussate, and in others, they are borne alternating in whorls of three. In both cases the leaves are fused basally to form a sheath at the node. Lateral branches are regularly produced in the axils of the leaves. The stem tends to be ridged and grooved in a manner somewhat suggestive of *Equisetum* and the distinctiveness of the nodes gives the stem a jointed aspect which further emphasizes this superficial similarity. During elongation the base of the internode remains meristematic longer than the upper regions and forms an intercalary meristem. This, according to Graham (1908-9), ultimately differentiates completely leaving in many cases an abscission layer several cells in thickness just above the node (PLATE I: 2) by means of which smaller branches are often shed at the end of the growing season.

MATERIALS AND METHODS

This study has been based on an examination of 6 two-leaved species and 3 three-leaved species of *Ephedra*. TABLE I indicates the origin of the specimens studied. Wherever possible a sample of the material used has been deposited in the herbarium of the Arnold Arboretum. Additional material of uncertain identity has also been examined.

In each case several series of sections of young growing tips were prepared. Serial sections of older material were also examined for comparison. In this way it was possible to follow the course of the leaf traces in the early stages of differentiation, and to evaluate the complications resulting from late differentiation and secondary activity. The distribution of bundles in successive transverse sections of each series was plotted and subsequently the longitudinal course of traces was reconstructed from these diagrams.

Fresh material collected at various times throughout the growing season, from 1948 to 1955, was fixed in formal acetic alcohol, medium chromo-acetic alcohol or Craf III (Johansen, 1940). A modified Zirkle's n-butyl alcohol method for dehydrating refractory plant material was employed and the material embedded by the paraffin-tissuemat method described by Pratt and Wetmore (1951). Transverse and longitudinal serial sections were cut at 8 to 10 micra on a Spencer rotary microtome. Haups' and

TABLE I

SPECIES	SOURCE	NO. OF VASCULAR BUNDLES IN INTERNODE **
Two-leaved species		
<i>Ephedra alata</i> * Dcne.	U.S.D.A. Plant Introduction Station, La Jolla, California	10
<i>Ephedra equisetina</i> Bge.	Arnold Arboretum, Jamaica Plain, Mass.; University of Manchester Greenhouse, Manchester, England	6, 7, 8
<i>Ephedra gerardiana</i> * Wall.	Arnold Arboretum, Jamaica Plain, Mass.; U.S.D.A. Plant Introduction Station, La Jolla, California	8, 9, 10
<i>Ephedra intermedia</i> * Schrenk. and C. A. Mey.	University of Manchester Greenhouse, Manchester, England	8, 9, 10
<i>Ephedra major procera</i> * Aschers. and Graebn.	Arnold Arboretum, Jamaica Plain, Mass.	8
<i>Ephedra viridis</i> * Cov.	Pipes Canyon, San Gorgonio Mts.; San Bernardino County, California	8, 10
Three-leaved species		
<i>Ephedra altissima</i> * Desf.	U.S.D.A. Plant Introduction Station, La Jolla, California	15, 17
<i>Ephedra californica</i> * Wats.	Morongo Canyon, Riverside County, California	15
<i>Ephedra chilensis</i> * Miers.	University of California Botanic Gardens, Berkeley, California (Grown from seed collected by J. West #5098)	15, 16

* Indicates that a specimen of the material used has been deposited in the herbarium of the Arnold Arboretum, Harvard University Herbarium, Cambridge, Mass.

** The italicized figures in the third column indicate the number of vascular bundles which occurs most frequently in the internodes of the material examined.

Mayer's adhesives (Johansen, 1940) were used to mount the sections. The slides were usually coated with a 0.5% solution of parlodion in ether, preparatory to staining.

The staining combinations employed were:

(1) Heidenhain's haematoxylin (0.5% aqueous) pre-mordanted in iron alum (4% aqueous), with 1% safranin in 50% alcohol as a counterstain (Jeffrey, 1917).

(2) 1% safranin in 70% alcohol, with picro-aniline blue (1 gm. water soluble aniline blue to 100 ml. of 80% ethyl alcohol with 1 ml. of saturated aqueous picric acid) as a counterstain.

(3) 1% safranin in 70% alcohol, counterstained with a saturated solution of cotton blue in lactophenol.

The parlodion coating was removed with acetone and the sections were cleared in xylol and mounted in damar in xylol in the usual way.

TWO-LEAVED SPECIES OF EPHEDRA

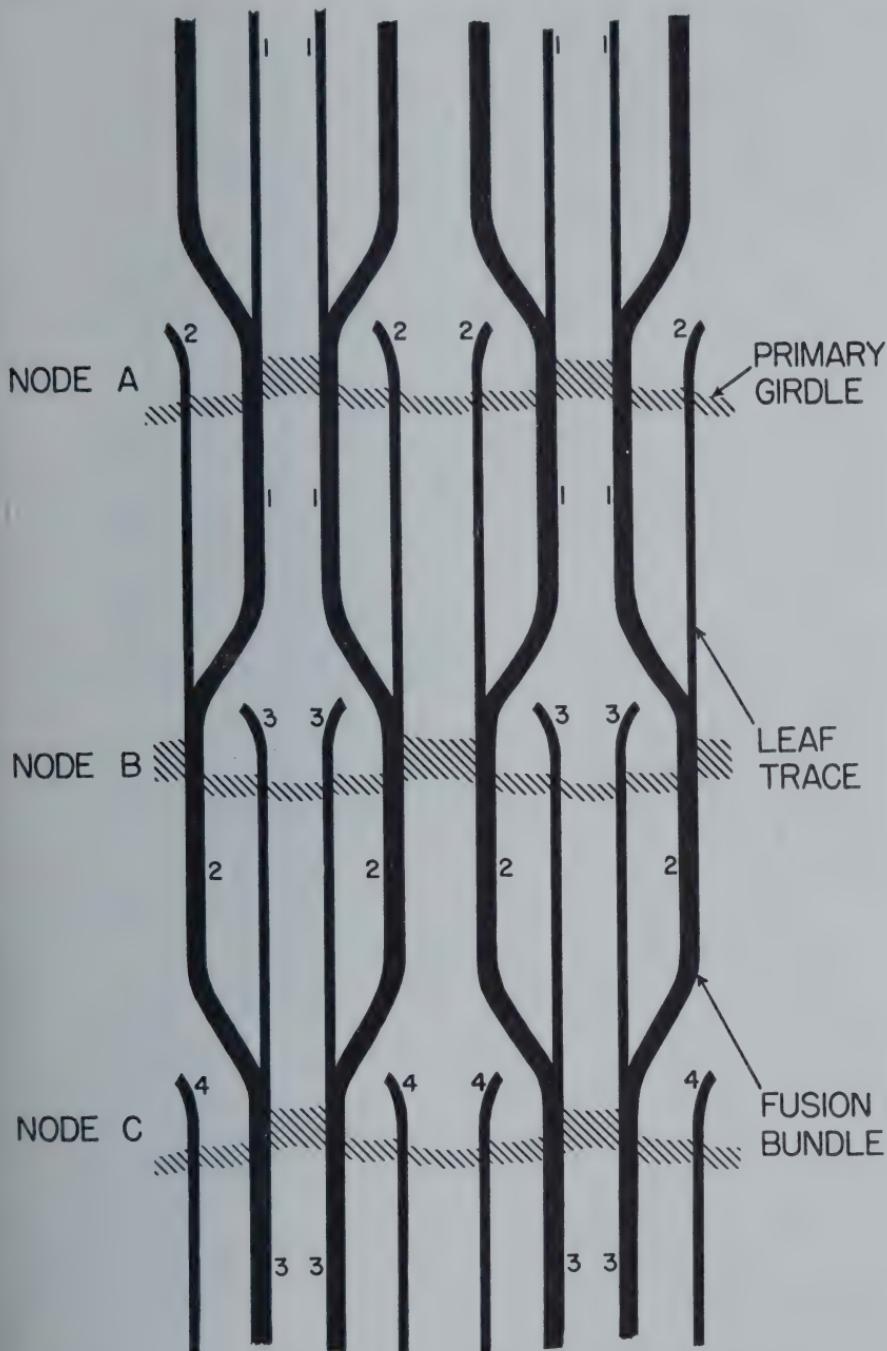
In the range of material examined in this study, a striking uniformity in primary vascular organization was found. It is therefore possible to describe the general pattern for two-leaved species without treating each one individually. Certain deviations from the general plan have been noted; but these represent minor discrepancies, often confined to a portion of a single shoot only.

Each leaf is supplied by two traces which remain separate, as far as could be determined, throughout the leaf. In the internode above a given node (e.g. FIG. 2:6), there are eight bundles in transverse section, two pairs (bundles B) directly opposite the leaves of the node below, and two pairs (bundles C) alternating with these. Just above the node the two bundles of each pair (B) facing the leaves at this node diverge towards the adjacent laterally placed bundles (C) (FIG. 2:7,8); and each fuses with one of these (FIG. 2:9) (FIG. 1 — bundle 2 above node B). As a result of this, there are, directly above the node, four fusion bundles in the transverse section (FIG. 2:9). These become associated in pairs at the node, laterally to the incoming leaf traces, and, through the intercalation of vascular elements, two "lateral crescents" of vascular tissue (FIG. 2:9,10) are formed. The two pairs of traces from the leaves of this node (e.g. traces C, FIG. 2:3; traces D, FIG. 2:10) now attach to the ends of these crescents. At the level of junction, there is no primary xylem between the two traces of each incoming pair (FIG. 2:3,10); but at a slightly lower level the "nodal girdle" is completed by the appearance of vascular tissue in these regions (FIG. 2:5,11). However, at this level the two fusion bundles in each lateral crescent (e.g. B in FIG. 2:5) have begun to separate into distinct strands.

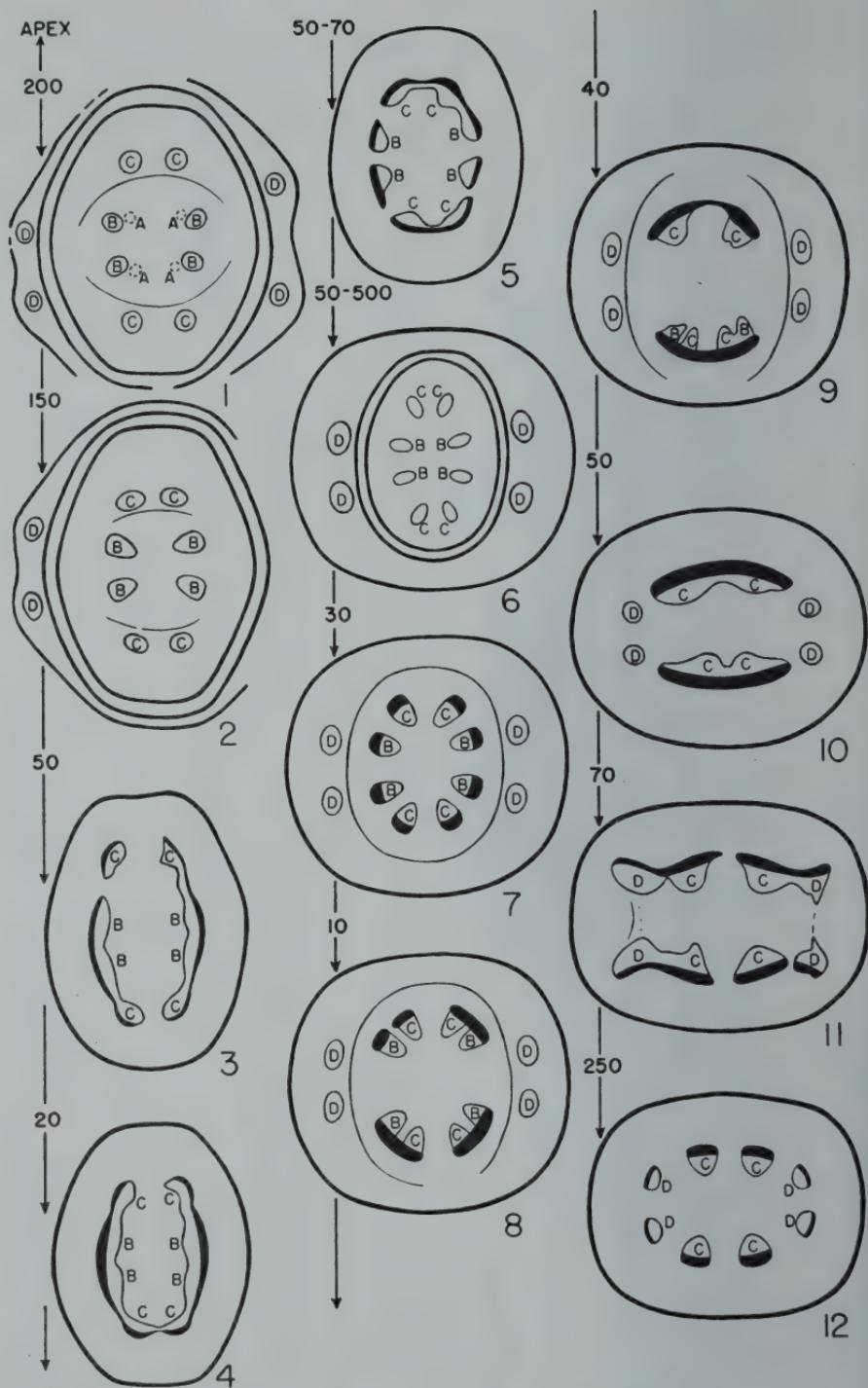
Below the node 8 distinct bundles are again present (FIG. 2:12). The two pairs of traces (D) from the leaves of the node above have continued through the nodal girdle, and alternate with two pairs of somewhat larger fusion bundles (C), which have also extended through the nodal girdle. The arrangement is much the same as that above the node, except that the pattern has been turned through 90° (cf. FIG. 2:6 and 12) (PLATE II, cf. 1 and 5).

Ephedra is characterized by the development at an early stage of conspicuous axillary buds. The several bundles in these buds unite laterally to form two traces in their course through the cortex of the main axis. These traces join to the lateral crescents of the nodal girdle on each side just above the level of leaf trace attachment. They appear to join the traces in these crescents rather than the incoming leaf traces, as has been suggested by Graham (1908-9).

From the description given above, it is apparent (FIG. 1) that the two



TEXT-FIGURE 1. A diagram of the longitudinal course of the primary vascular strands through three nodes in the stem of a two-leaved species of *Ephedra*. The diagram is constructed to show the strands spread out in one plane. The extent of primary xylem in the nodal girdle is shown by striping.



TEXT-FIGURE 2. A series of transverse sections through a young stem of *Ephedra viridis*. Procambium is shown within the dotted lines. The area within the solid lines represents the extent of the primary xylem. Secondary tissue is shown in solid black. No attempt has been made to show the primary phloem. Consecutive sets of two pairs of vascular bundles entering the stem as leaf traces are designated by letters in sequence. The distance in micra between sections is shown on the left.

traces (e.g. traces No. 2) from any given leaf, after entering the stele, extend vertically through the internode below. Just above the next node (B) they (traces No. 2) are joined by the bundles of the leaves two nodes above (traces No. 1). Since the combined bundles subsequently follow the same vertical course as the original traces (No. 2), and since the bundles which join them (No. 1) diverge from their course in so doing, it seems reasonable to consider these combined bundles as further extensions of the leaf traces. This terminology would appear to be in keeping with that of Esau (1943) for *Linum*. The traces (No. 2) extend through the node (B) and the succeeding internode; and, just above the next node (C) diverge, each joining with a trace (No. 3) from a leaf one node above (B) (that is, one node below that at which they themselves pass out into the leaves). Each leaf trace thus has a vertical extent in the stem of nearly two internodes; and the two traces from any one leaf join the traces of two separate leaves from the node below. It is apparent from the reconstruction of FIGURE 1 that there are in the stems of two-leaved species of *Ephedra* four essentially independent vascular systems, and that the two traces of any given leaf are derived from two of these.

This interpretation of the primary vascular system of *Ephedra* is essentially in agreement with that given by Nägeli (1858), Geyler (1867-68, p. 196) and Strasburger (1872). It differs from that of Graham (1908-9) in that he believed that the leaf traces, after a vertical course of two internodes in the stem, fuse with the traces of the leaves which are attached at the second node below that of their own departure from the stele. There is, however, an even sharper divergence between the interpretation given here and that of Thompson (1912), who held that the leaf traces arise directly from the girdle at each node. He did, however, indicate that in some cases a local thickening of the girdle suggested a weak connection between a leaf trace and a bundle in the internode below. The difference of opinion clearly rests upon an interpretation of the nodal girdle.

In an examination of mature regions of the stem it is difficult to determine the continuity of bundles through the nodal girdle. However, if one examines immature regions of the stem, the phenomenon is easier to observe. In all species examined there was no doubt that the leaf traces, at the node of their insertion, formed only a transitory association with the girdle, never lost their identity in it, and continued as distinct bundles in the internode below. At the node below, after being joined by the traces of leaves from one node above their own departure, the fusion bundles on each side appear to merge to form the lateral crescents (PLATE II:3). In some cases it is difficult to follow them through the lateral crescent. However, in other cases, particularly in immature material, it is clear that they do extend through the crescent, and this view is enhanced by the fact that the corresponding large bundles in the internode below coincide in position with the fusion bundles just above the node (PLATE II: cf. 2, 3 and 5).

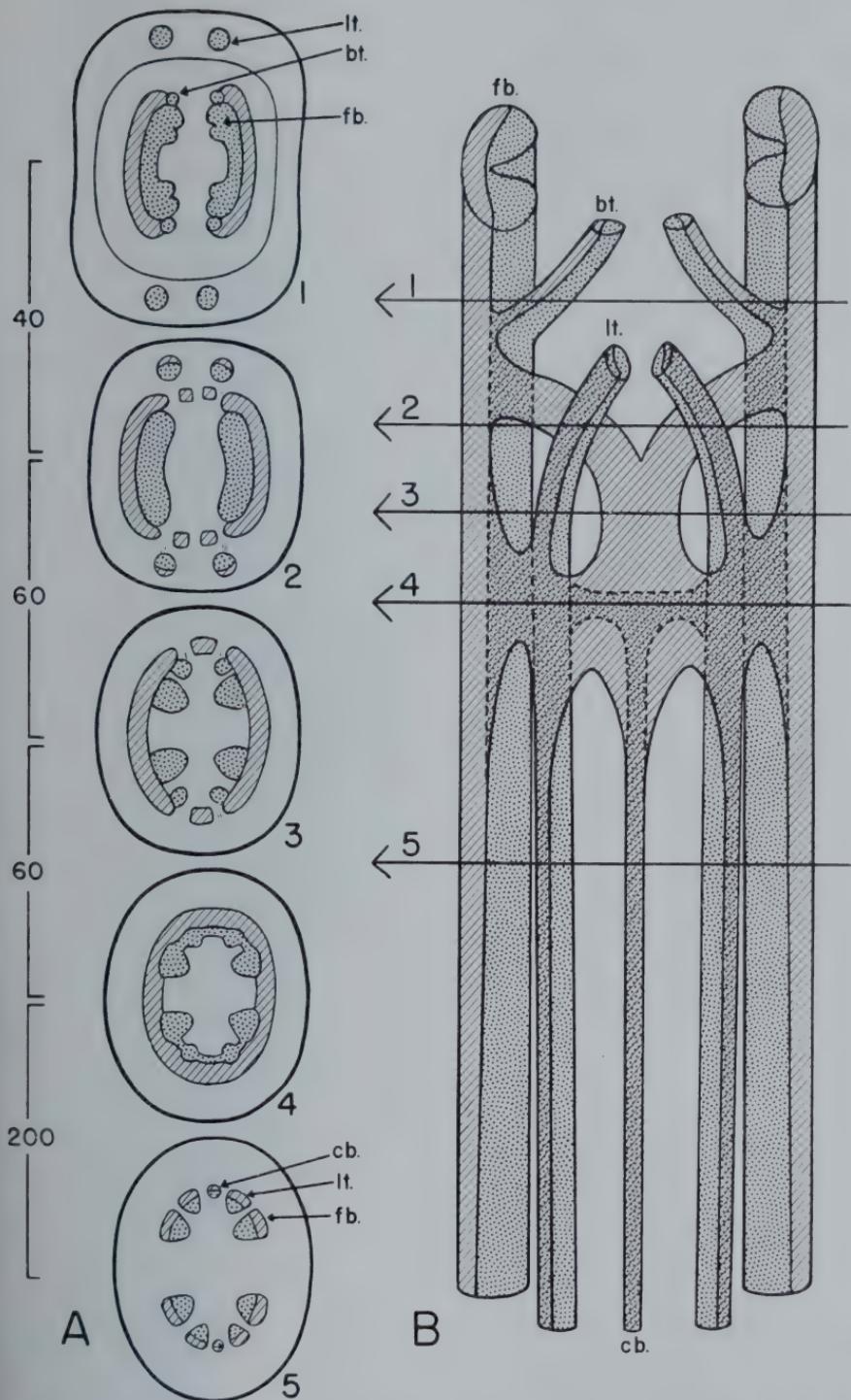
An examination of longitudinal sections of the node shows the nature of the girdle (PLATE I:2). It is composed for the most part of relatively

isodiametric tracheids somewhat resembling transfusion tissue. The vascular bundles appear, however, to be continuous through this tissue. The elements in the bundles are broader and shorter than those in the internodal portions; but they are distinctly longer than those of the girdle wood between bundles (PLATE I:2). This broadening of the elements of the bundle is particularly pronounced in any leaf trace at the node below its insertion, that is when it is a fusion bundle. This explains the difficulty in tracing the fusion bundles through the lateral crescents.

The structure of the nodal region is complicated by an additional phenomenon, the early initiation of cambial activity. Cambial activity has been observed as close to the apex as the third node in some cases, although frequently it is later in its appearance. It is of interest that secondary activity is initiated separately at each node, and subsequently spreads through the internodes above and below. Cambial activity soon superimposes a heavy nodal girdle of secondary tissue upon the primary structure and adds to the difficulty of tracing bundles through the node.

Secondary tissue alters the appearance of the departure of the leaf traces and has led to some confusion. The primary tissue of the nodal girdle is apparent between the two traces of a given leaf only below their attachment to the lateral crescents. Above their departure there is a single gap, and the node is distinctly unilacunar (PLATE II:3). Cambial activity, in addition to thickening the girdle between the two recently attached traces, spreads upward between them at an early stage forming a mass of secondary wood at and above the point of departure (FIG. 3). In mature nodes of *E. viridis* this "bundle" of secondary wood was observed to split above the level of departure of the leaf traces, one half attaching to the secondary portion of the lateral crescent on each side (FIG. 3), just below the departure of the two branch traces. Thus the two leaf traces appear to have separate gaps as figured by Thompson (1912), but these gaps are in the secondary body and the only vascular tissue between the departing traces is secondary. This condition in *Ephedra* has been referred to by Sinnott (1914).

Although the basic primary vascular system of two-leaved species of *Ephedra* provides for eight bundles in the internode, it is apparent (Table I) that considerable variation occurs. Variation may even be noted in different portions of the same branch. This variation was observed by earlier workers, notably Strasburger (1872), Graham (1908-9), and Liu (1929). A reduction from the basic number of eight, particularly common in *E. equisetina*, occurs by the formation of what Graham (1908-9) has called "concrescent" bundles. After their association in the lateral crescent at the node below their insertion, the two leaf traces of a given pair fail to separate into distinct bundles, and are represented during the second internode of their vertical course by a single bundle only. The occurrence of this phenomenon on one or both sides of the axis gives rise to the 6- or 7-bundle condition (see PLATE I:3). At the node below, where the two traces normally diverge, the concrescent bundle usually divides into two



TEXT-FIGURE 3. Diagrams of transverse sections and longitudinal course of primary (stippled) and secondary (striped) vascular tissues of a mature node of *Ephedra viridis*. Only the vascular strands on the near side of the stem (which is the side where a leaf is inserted) are shown in the longitudinal diagram. The distance in micra between the sections in A is shown on the left. fb. = fusion bundle; bt. = bud trace; lt. = leaf trace; cb. = complementary (accessory) bundle. Note the positions of the primary and secondary girdles.

parts, one part fusing with a trace on each side. However, less frequently, the entire bundle diverges to one side and fuses with one trace.

The occurrence of 9 or 10 bundles requires a different explanation. This is provided by the "complementary" or "accessory" bundles noted by Strasburger (1872) and by later workers. Located between the two traces of a leaf, this complementary bundle extends from the nodal girdle where the leaf traces enter the stem to the lateral crescent between these two traces at the node below. It does not appear to anastomose with the leaf traces at any level. Accompanying one or both pairs of leaf traces, such bundles produce the 9- and 10-bundle condition (PLATE I:4).

THREE-LEAVED SPECIES OF EPHEDRA

The three-leaved species examined in the course of this study exhibit a degree of uniformity comparable to that of the two-leaved species. The general pattern is similar to that of the two-leaved species, but involves a larger number of bundles. The increased number of bundles results from the presence of an additional leaf at each node, and from the regular occurrence, in the three species examined, of complementary bundles. Graham (1908-9), however, reported that the complementary bundle does not always occur in three-leaved species of *Ephedra*.

Typically, in the internode above a given node, fifteen bundles are seen in transverse section (PLATE III:1). Three groups of three bundles, each group consisting of the pair of traces from a leaf of the first node above accompanied by a complementary bundle, alternate with three pairs of somewhat larger bundles, which are the leaf traces of the leaves of the second node above. In the upper regions of the stem the complementary bundles are frequently not yet differentiated, so that only twelve bundles are present in the internode (FIG. 5:3). Just above the node, the paired bundles which are opposite the leaves of this node diverge and each fuses with the trace adjacent to it, so that there are now three pairs of fused bundles, each with a complementary bundle between the two members (PLATE III:2). Each pair is then joined by vascular elements of the nodal girdle, forming three crescents lateral to the incoming leaf traces (e.g. FIG. 5:6). In immature nodes, the crescents are often not present (PLATE III:2,3), and the fusion bundles remain distinct through the node. The complementary bundles terminate in the crescents without joining either leaf trace, as in the two-leaved species having extra bundles. The incoming traces take up their position in the stele and form a transitory connection with the lateral crescents (FIG. 5:6,7) (PLATE III:3). In many cases the bundles in the crescents separate before the connections of the incoming traces are formed. At a slightly lower level, below the insertion of the traces, a band of nodal xylem is apparent between the two traces (FIG. 5:7,8) (PLATE III:4). There is thus a complete nodal girdle, but it is not seen as such at any one level since the connections between the fusion bundles usually do not occur at the same level as the connections between the incoming traces.

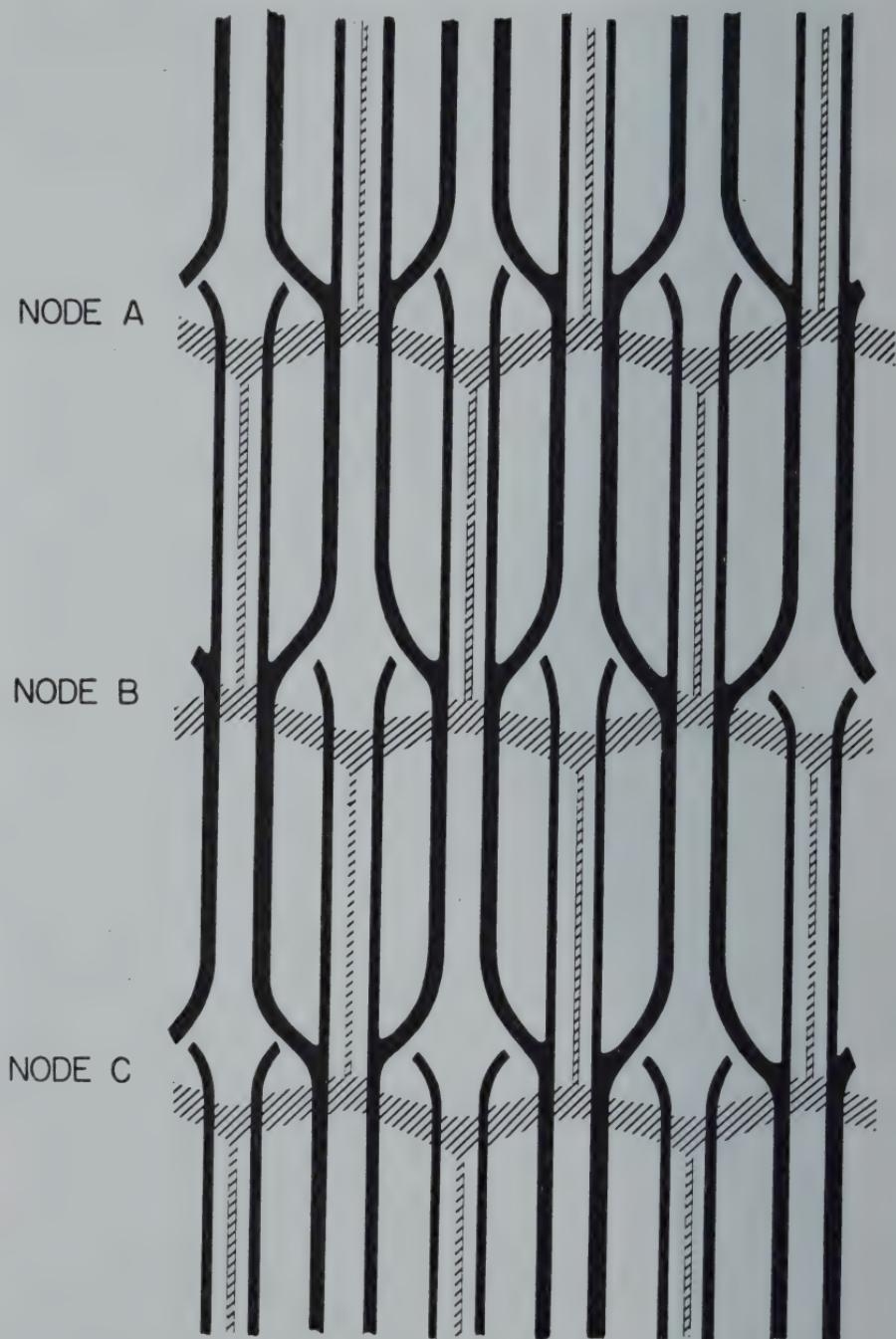
Below the node, the bundles are again distinct, with six pairs of larger bundles clearly representing the fusion bundles from above the node, and three groups of three smaller bundles which are the leaf traces of the last node, each pair accompanied by a complementary bundle (FIG. 5:9). The complementary bundle originates in the nodal ring between the traces. Occasionally extra complementary bundles are formed (FIG. 5:9) so that sixteen or more bundles may be present in the internode.

It is apparent from this description that, as in the two-leaved species, each leaf trace has a vertical extent of nearly two internodes in the stem (FIG. 4). It is joined at the second node by the trace of a leaf one node above its own insertion, and at the third node itself joins the trace of a leaf one node below its own insertion. There are, in the stems of the three-leaved species of *Ephedra*, six independent vascular systems; each leaf is supplied by traces derived from two of them. The three-leaved species are, like the two-leaved, unilacunar, there being no primary vascular tissue between the two traces at or above the level of insertion. (PLATE III:3). The early appearance of cambial activity complicates the nodal structure, forming a heavy ring of secondary tissue. Secondary activity spreads upwards between the departing leaf traces, forming between them a band of secondary wood in mature nodes. The departing traces then leave two gaps in the secondary body.

The regular occurrence of a complementary bundle makes possible a more detailed consideration of its structure and significance than was possible in the two-leaved forms. The complementary bundle has been observed repeatedly extending from nodal girdle to nodal girdle without in any way joining the leaf traces. However, in several cases in *E. altissima*, individual leaves having three traces were observed. In all cases the median trace was continuous below with the complementary bundle. The behavior of the lower portion of this bundle under these conditions was in no way different from the normal condition. The significance of this three-trace leaf vasculature is not clear. Monoyer (1938) has reported three traces in the leaves of *E. fragilis*. Graham (1908-9) states that the complementary bundle extends upwards through the node, divides, and provides accessory vasculature for the lateral bud. It seems probable that this author has misinterpreted the secondary tissue between the departing traces (cf. FIG. 3) as an upward extension of the complementary bundle.

DISCUSSION

The primary vascular system of *Ephedra* seems best interpreted as a eustele in which the internodal bundles are continuous with the leaf traces. The rather anomalous occurrence of a girdle of nodal wood, through which the leaf traces must be considered to pass, poses certain objections to this interpretation. Thompson (1912) has in fact concluded that the leaf traces cannot be followed through this girdle. At an early stage of differentiation, however, the continuity of strands through the girdle seems quite clear, and the additional nodal vascular elements have the appearance of



TEXT-FIGURE 4. A diagram of the longitudinal course of the primary vascular strands through three nodes in the stem of a three-leaved species of *Ephedra*. The diagram is constructed to show the strands spread out in one plane. The extent of primary xylem in the nodal girdle is shown by striping. Note the complementary or "accessory" bundles (also shown striped).

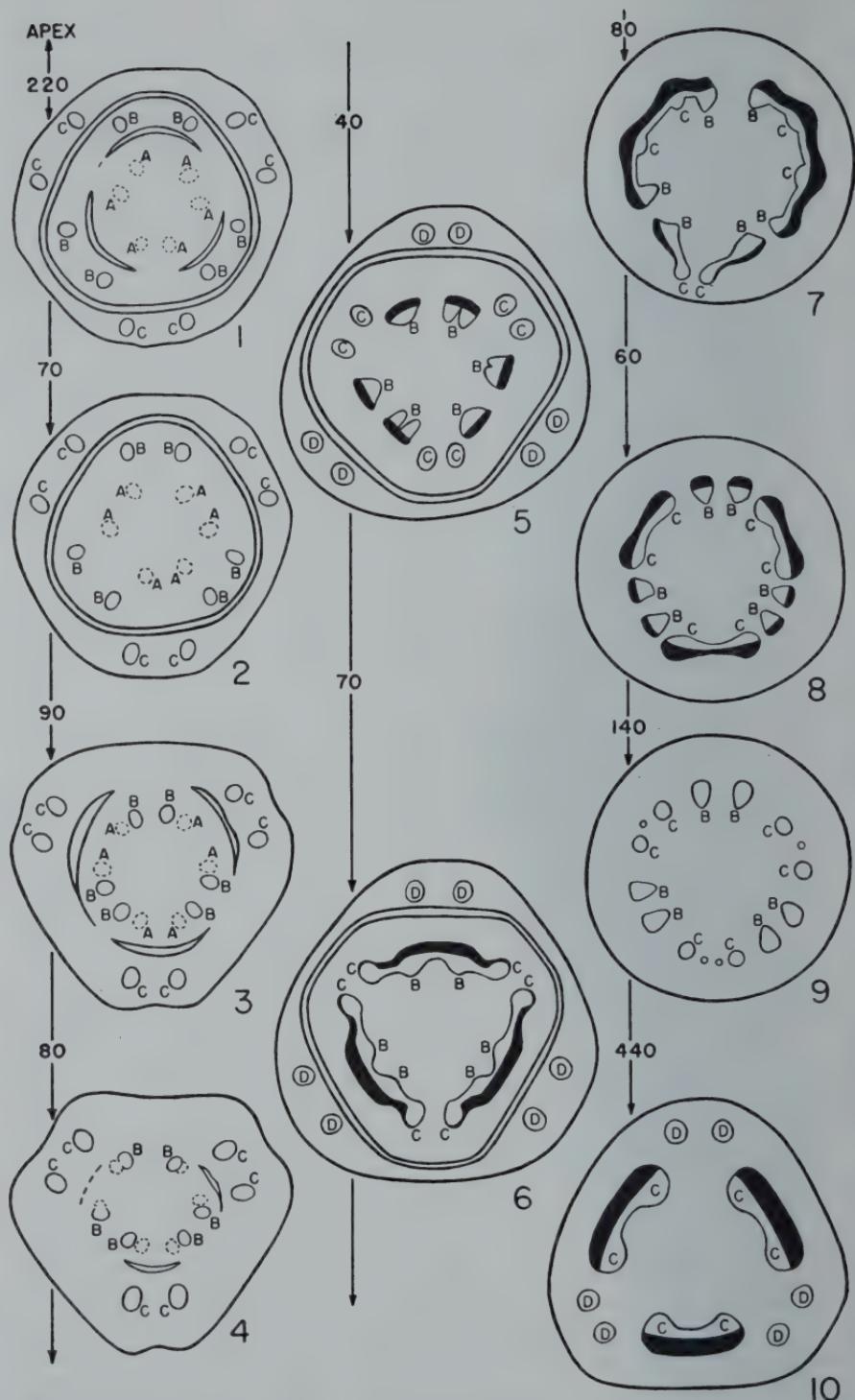
being intercalated between the leaf traces. This appearance is striking, in spite of the relatively early differentiation of the girdle, because of the peculiar form of its elements. These are nearly isodiametric in shape and bear a strong resemblance to those of transfusion tissue. The bundles can be traced through this girdle in longitudinal section by the relatively elongate nature of their tracheary cells. In the nodal region, however, even the elements of the bundles are somewhat shorter and wider than they are in the internodal region. Possibly this general shortening of elements at the node is related to the non-elongation of this region, as compared to the extensive elongation of the internodes. The nodal girdle would appear to be a specialized feature superimposed upon the basic eustelic pattern, possibly in relation to some physiological necessity.

The superficial resemblance of *Ephedra* to *Equisetum* in external characteristics is paralleled, as many workers have noted, by a similarity of internal organization, particularly in the occurrence in both of a nodal ring of relatively short vascular elements. It is interesting, and perhaps significant to the present study, that the interpretation given here of the relation of the leaf traces to the nodal girdle closely resembles that offered by Golub and Wetmore (1948) for *Equisetum*, on the basis of a developmental study.

Further support for this interpretation of the primary vascular system of *Ephedra* is provided by the close correlation between the leaf number and arrangement at the node and the bundle pattern in the internode below. The difference in internal organization between two- and three-leaved species is clearly related to the difference of leaf number. Moreover, Bertrand (1874, p. 20) reported that in material of *Ephedra triandra* having four leaves at each node, there are eight pairs of bundles in the internode. This is the pattern which would be expected for a stem bearing four leaves at each node, assuming that there are no complementary bundles. Graham (1908-9) has further stated that in stems in which the leaf number changes from two to three, corresponding differences may be noted in the internodal bundle pattern. In the present study no material possessing four leaves at the node has been observed, nor have any stems showing changes in leaf number been encountered.

On the other hand, the occurrence of complementary bundles extending from the girdle at one node to the girdle at the next, would seem to disprove a close correlation between the leaves and the internodal vascular bundles. Except in rare cases in which the complementary bundle extends into the leaf as a third trace, it has no connection with the leaf traces. The complementary bundles would appear to be, like the nodal girdle, an accessory structure superimposed upon the basic eustelic pattern. This view is supported by the relatively late differentiation of complementary bundles in comparison with the leaf traces. They are often not distinguishable in any form in the first several internodes at the tip of a stem, even though the leaf traces are clearly recognizable at this level (see FIG. 5:3).

In the two-leaved species of *Ephedra*, there are four quite separate vas-



TEXT-FIGURE 5. A series of transverse sections through a young stem of *Ephedra chilensis*. Procambium is shown within dotted lines. The area within the solid lines represents the extent of the primary xylem. Secondary tissue is shown in solid black. No attempt has been made to show primary phloem in the strands. Consecutive sets of three pairs of vascular bundles entering the stem as leaf traces are designated by letters in sequence. Note the appearance of complementary (accessory) bundles in section 9. The distance in micra between sections is shown on the left.

cular systems. Each of these four systems supplies half the vascularization of one of the pair of leaves at every node. Similarly in the three-leaved species there are six separate vascular systems, each of which contributes half the vascular supply to one of the three leaves at every node. These vascular systems are basically similar to those exhibited by a number of other plants, particularly among the Gymnospermae and Angiospermae. In *Ginkgo biloba*, for example, it has been reported (Gunckel and Wetmore, 1946a and b) that there are two distinct foliar traces supplying each leaf in both long and short shoots. These traces depart through a single gap in the stele. Gunckel and Wetmore (1946b) figure the connection of each foliar trace to an independent bundle of the eustele.

Prof. I. W. Bailey and his students have demonstrated the occurrence of this two-trace unilacunar condition in several ranalian families, for example, in the Austrobaileyaceae (Bailey and Swamy, 1949), Monimiaceae (Money, Bailey and Swamy, 1950) and Chloranthaceae (Swamy and Bailey, 1950; Swamy, 1953). Further, this nodal condition is known to occur widely throughout other dicotyledonous families (Marsden and Bailey, 1955) in both the adult and seedling conditions.

In *Austrobaileya*, the opposite leaves are supplied by two pairs of strands through unilacunar gaps in the stele (Bailey and Swamy, 1949). The two foliar traces are independent from one another below the node and arise from two different strands of the eustele. As in the two-leaved species of *Ephedra*, there are four separate vascular systems. Similarly, in *Trimenia*, four separate vascular systems supply the decussately arranged leaves. Each leaf is vascularized by two distinct traces which depart through a unilacunar gap in the stele as in *Ephedra*, *Austrobaileya* and *Ginkgo*; and the leaf traces arise from independent strands in the eustele. Similar conditions have been recorded for *Ascarina*, *Hedyosmum* and *Chloranthus* (Swamy, 1953).

The leaf traces of *Ephedra* have been figured as having two separate gaps at the node (Thompson, 1912; Sinnott, 1914). It has been shown in the present investigation that this "bilacunar" condition is a superimposed one since it occurs only in the secondary vascular tissue and not in the primary body. A similar condition occurs in *Trimenia*. At the node in *Agathis spinulosa* and *Mesoxylon sutcliffi* (Thompson, R. B., 1913) the two foliar traces are separated by a wedge of secondary wood. Thus in all of these cases the node basically shows a unilacunar, two-trace condition.

The vascular pattern in *Ephedra* poses a number of significant questions which might be answered by a developmental study. An understanding of the unusual nodal structure of this genus can only be obtained from an investigation of the development of the nodal girdle in relation to the leaf traces which extend through it. The possible importance of the non-elongation of the node in this connection has already been mentioned. Similarly, the early and separate initiation of cambial activity at the nodes is a phenomenon which deserves further study, particularly in view of the profound influence of this secondary growth upon the structure of the node. The delayed differentiation of the complementary bundles has been noted

earlier. A thorough study of the differentiation of the complementary bundle, including cases in which it appears to become incorporated into the leaf vasculature as an extra trace, would seem to be required. A developmental study of *Ephedra*, particularly directed along these lines, is now being undertaken.

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HARVARD UNIVERSITY.

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EXPLANATION OF PLATES

PLATE I

1. Habit of *Ephedra viridis* growing in the greenhouses of the Harvard Biological Laboratories.
2. Longitudinal section of a node of *Ephedra* sp., showing the nature of the elements of the nodal girdle and the continuity of a bundle through it. The bundle on the left is a leaf trace passing through the lateral crescent at the node below its departure from the stele. The short girdle elements appear to project towards the center because of the obliquity of the section ($\times 70$).
3. Transverse section of an internode of *Ephedra equisetina* showing the six-bundle condition ($\times 100$).
4. Transverse section of the stem of *Ephedra gerardiana* showing ten bundles in the internode ($\times 70$).

PLATE II

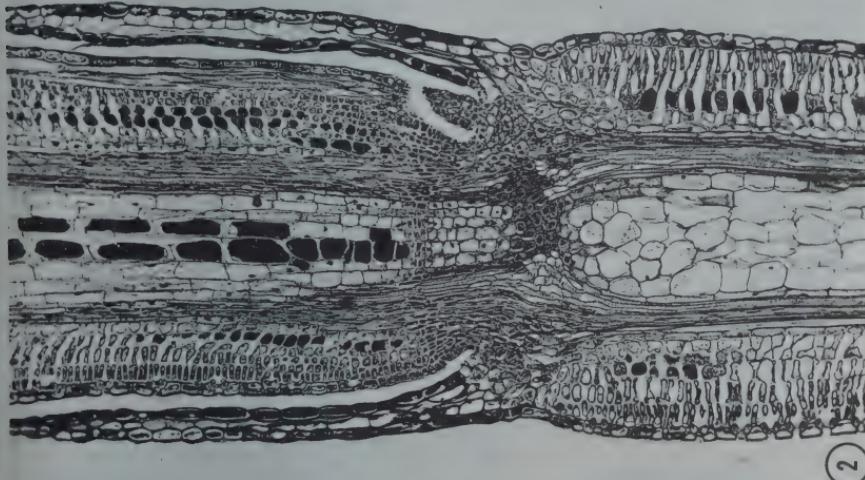
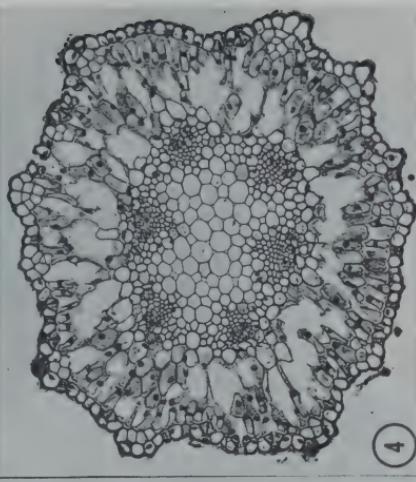
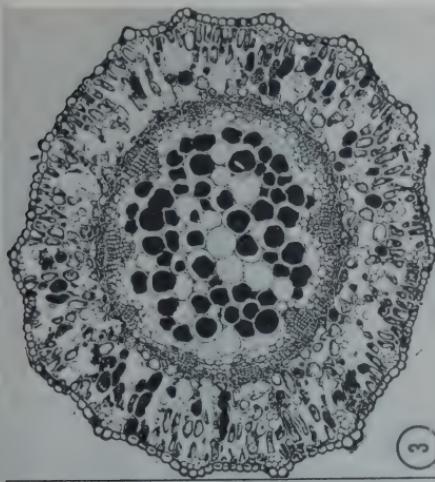
SERIES OF TRANSVERSE SECTIONS THROUGH AN IMMATURE NODE OF *Ephedra gerardiana*.

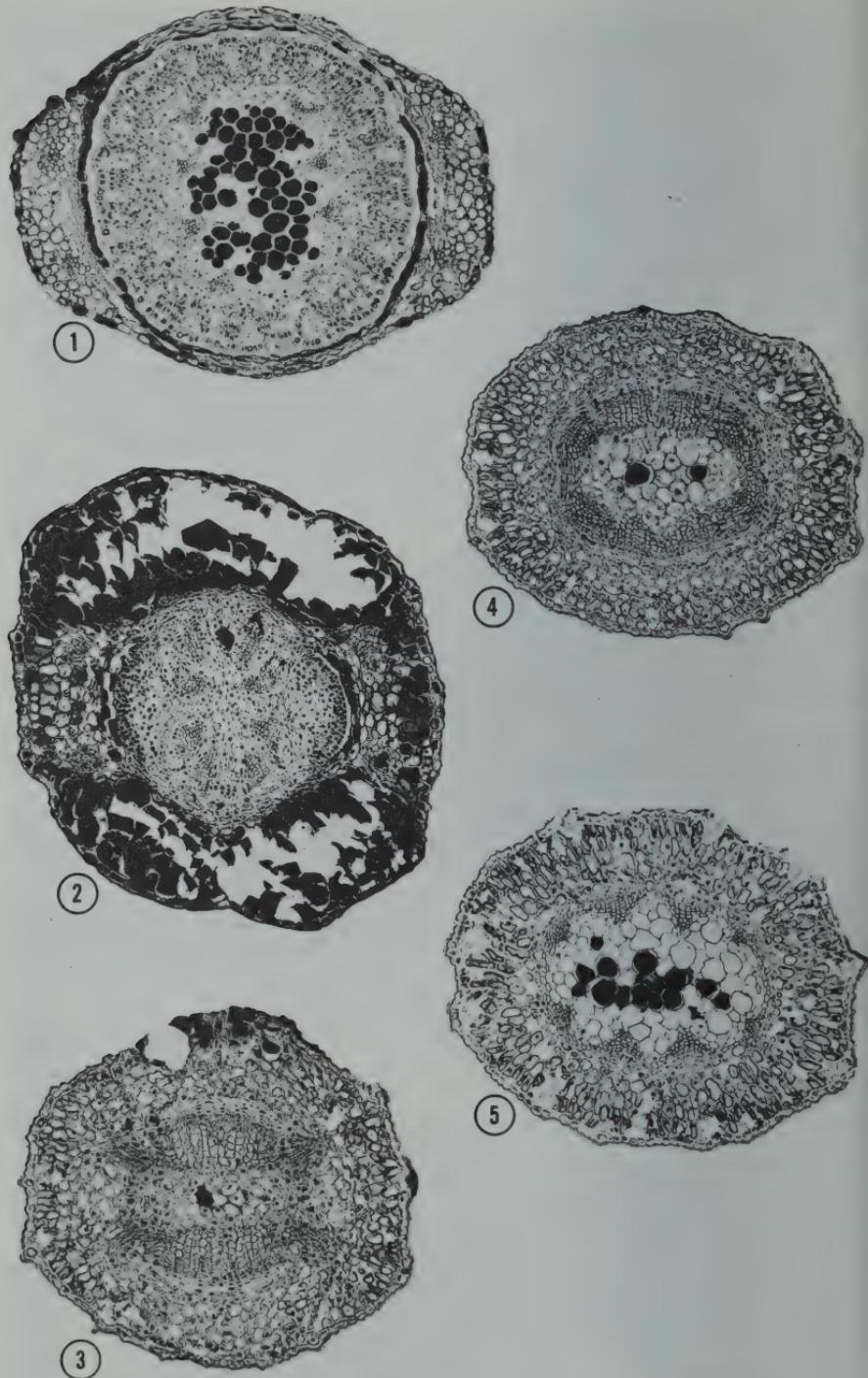
1. Internodal section with eight bundles ($\times 70$).
2. Just above the node showing the divergence of the traces of leaves two nodes above, towards the traces of the leaves one node above ($\times 70$).
3. Section at the node, with two lateral crescents and paired leaf traces attaching at their ends. Note evidences of cambial activity in the crescents ($\times 70$).
4. A slightly lower level showing a nearly complete nodal girdle. The traces in the lateral crescents have begun to separate. Note evidence of cambial activity ($\times 70$).
5. Below the node, with eight distinct bundles again present ($\times 70$).

PLATE III

SERIES OF TRANSVERSE SECTIONS THROUGH AN IMMATURE NODE OF *Ephedra altissima*.

1. Internodal section with fifteen bundles ($\times 60$).
2. Just above the node showing fusion of traces from leaves two nodes above with traces of leaves one node above. Note the complementary bundles ($\times 60$).
3. Nodal section showing the attachment of incoming leaf traces. In this immature region of the stem no lateral crescents have been formed ($\times 60$).
4. A slightly lower level, showing bands of primary xylem between pairs of recently attached leaf traces ($\times 60$).







THE OCCURRENCE OF EUPTLEA IN THE CENOZOIC
OF WESTERN NORTH AMERICA

RICHARD A. SCOTT AND ELSO S. BARGHOORN

With three plates

IN THE EOCENE CLARNO FORMATION of north central Oregon logs and numerous fragments of silicified wood occur in association with fruits and seeds. The Clarno formation, one of a series of early Tertiary deposits in the basin of the John Day River, consists of interbedded conglomerates, tuffs, ash layers and lava flows. In very limited outcrops of the formation, in beds of siliciously cemented volcanic tuff, numerous seeds and fruits may be found. These are preserved chiefly in the form of chalcedony filled locule casts, and retain in minute detail the internal morphology and anatomical structure of a wide range of angiosperm seeds and fruits. The seed flora, insofar as it has been studied, has been described and interpreted in an intensive investigation by Scott (1954 and unpublished mss.). The tissues of the silicified logs and more abundant fragments of silicified wood which accompany the seeds and fruits are remarkably well preserved in many cases, and in both external form and internal organization the logs and fragments show evidence of silicification prior to compression failure from the weight of overlying sediments. The bulk of the preserved stems are decorticated, and commonly, in thin section, show evidence of extensive fungus attack on the wood, hence indicating conditions of aerobic decomposition preceding burial and mineralization.

The Clarno woods are being intensively studied with regard to their botanical identification and interpretation, and a number of genera have now been determined. Among the genera thus far recognized is one of unusual interest from the standpoint both of its morphology and its geographic distribution, viz., the genus *Euptelea*. As far as the authors are aware this occurrence comprises the first fossil record of the genus. The existence of *Euptelea* in the early Tertiary of western America constitutes another significant addition to the growing body of paleobotanical evidence relating the early Tertiary forest history of North America to that of southeastern Asia.

Euptelea is one of a group of small or monotypic genera extant today only in warm temperate and subtropical eastern Asia. Other members of this morphologically and geographically isolated group of woody plants include *Cercidiphyllum*, *Trochodendron*, *Tetracentron*, and *Eucommia*. These five genera have been variously associated taxonomically in the past (Swamy and Bailey 1949), but comprehensive anatomical study has revealed numerous and significant divergences in structural organization and floral morphology among them, demonstrating convincingly that each

genus is best regarded as constituting a distinct family (Tippo 1940; Nast and Bailey 1945; Nast and Bailey 1946; Swamy and Bailey 1949).

The genera constituting the Trochodendraceae, Tetracentraceae, Cercidiphyllaceae and Eupteleaceae possess in common certain ranalean characters in one or more of their organs or parts. The vesselless Trochodendraceae and Tetracentraceae are closely related, having many morphological features in common. On the other hand, the Cercidiphyllaceae and Eupteleaceae are quite distinct from each other and, likewise, quite distinct from the vesselless *Trochodendron-Tetracentron* complex. The genera included in these four families logically may be regarded as relics of ancient ranalean origin which have evolved independently at least since Upper Cretaceous time, and probably will ultimately be found to have been distinct in older Upper Cretaceous deposits. That three of these genera, excluding *Euptelea*, have been in existence in post Cretaceous time as essentially "modern" entities is well documented by their occurrence in Tertiary deposits. *Cercidiphyllum* is known from the Middle Eocene of England, the Eocene of Greenland and from numerous horizons in the early and middle Tertiary of continental United States (Brown 1939). Vesselless dicotyledonous woods conforming in structure to either or both *Trochodendron* and *Tetracentron* have been found in the Eocene of Greenland (Mathieson 1932), the Oligocene of Oregon (Hergert and Phinney 1954) and the Miocene of Washington (Beck 1941, 1944). Fruits apparently belonging to *Trochodendron* have been described from the Eocene of England (Reid and Chandler 1933).

Hence, with the notable exception of *Euptelea*, there is well documented evidence that these presently Asiatic genera once grew on the American continent and were quite probably Holarctic or circumboreal in distribution. Recognition of *Euptelea* among this assemblage of phylogenetically and geographically isolated primitive angiosperms adds measurably to our understanding of the diverse character of the woody flora of early Tertiary temperate and high latitudes in North America and accentuates the degree of depauperization which took place during the late Cenozoic. It is quite probable that further additional components of the highly diversified woody angiosperm flora currently surviving in warm temperate Asia will be found among the early Cenozoic fossil floras of temperate America. Indeed, the question may be asked whether many of these genera are not already known as leaf impressions, but are concealed in fossil floras by mis-applied binomials or form generic names, as was clearly demonstrated by Brown (1939) in the case of the American Cenozoic record of *Cercidiphyllum*.

Assignment of the fossil wood under consideration to *Euptelea* is as follows:

***Euptelea baileyana* Scott & Barghoorn sp. nov.¹** (PLATE I, FIG. 1; PLATE II, FIG. 1; PLATE III, FIGS. 1, 2, 3.)

¹ This species is named in recognition of Professor Irving W. Bailey's contributions in establishing the morphological and taxonomic position of the phylogenetically isolated genus *Euptelea*.

VESSELS: Small, mean tangential diameter 54 μ , somewhat smaller in the late wood; chiefly solitary, occasionally paired, or appearing paired as a result of overlapping of vessel elements; about 85 per sq. mm. in the early wood, somewhat more abundant in the late wood. Thin walled; oval or slightly angular in transverse section. Vessel elements up to 0.85 mm. long. Perforation plates oblique, exclusively scalariform; bars mostly narrow and widely spaced, varying in number from 5 to 35, most commonly about 15, per perforation plate. Intervascular pit pairs predominantly scalariform with narrow apertures, occasionally opposite. Pits to parenchyma scalariform, the apertures wider than those of the intervacular pits. Numerous thin walled tyloses present. Vessel distribution graded porous.

PARENCHYMA: Very scanty diffuse.

RAYS: Heterogeneous (Kribs Type IIA); multiseriate rays up to 18 cells wide and 2 mm. high, with 1 to 6 marginal rows of enlarged isodiametric or upright cells; uniseriate rays 2 to 7 cells high, composed chiefly of upright cells but occasionally including 1 or more almost procumbent cells; up to 8 per mm.

IMPERFORATE TRACHEARY ELEMENTS: Thick walled fiber tracheids, the pits with small but distinct borders.

LOCALITY AND GEOLOGIC OCCURRENCE: SE $\frac{1}{4}$ sec. 27, T. 7 S., R. 9 E., Wheeler Co., Oregon. Middle (?) Eocene, Clarno formation.

COLLECTOR: Richard A. Scott, July 1950.

MATERIAL: A single specimen of silicified, mature, secondary xylem measuring approximately 2 x 2 x 2 cm. The curvature of the growth rings indicates that the stem, of which this specimen represents a small fragment, had a diameter of at least 10 cm.

HOLOTYPE: University of Michigan, Museum of Paleontology, No. 32338. represented by three ground sections. Three ground sections are also deposited in the Paleobotanical Collections, Harvard University, No. 55572.

AFFINITIES AND DISCUSSION

Structural features of the fossil wood indicate, after extensive comparison, that its closest affinities are with the modern genus *Euptelea*. There is close agreement in all details except those noted below. The fossil wood shows a superficial resemblance to the mature secondary xylem of *Platanus*, particularly as seen in the transverse plane of section. However, the broad rays of *Platanus* are homogeneous, whereas the fossil possesses conspicuously heterogeneous multiseriate rays.

The secondary xylem of the two living species of *Euptelea*, *E. polyandra* Sieb. & Zucc. and *E. pleiosperma* Hook f. & Thoms. is characterized by small, predominantly solitary vessels. There is a conspicuous difference in diameter between the vessels of the early wood and those of the late wood (PLATE I, FIG. 2). The size and distribution of the vessels of *E. baileyana* agree with the distributional pattern in the two modern species. Mean tangential diameter of the vessels in the fossil specimen is intermediate between the measurements secured from comparable secondary xylem

of the two modern species, as follows: *E. polyandra* 52 μ , *E. baileyana* 54 μ and *E. pleiosperma* 57 μ . Thin walled tyloses, present in the vessels of both living and fossil species, appear more abundantly in the fossil. These structures tend to tear out in the sectioning and manipulation of unimbedded wood and hence for this reason there is artificially introduced a slight difference in appearance of the wood of the fossil and living forms.

The two major differences between the vessel elements of the modern and fossil species are in the structure of the intervacular pit-pairs and in the number and spacing of the bars in the scalariform perforation plates. In both the extant species the intervacular pitting is transitional between scalariform and opposite-multiseriate, whereas in the fossil form it is chiefly scalariform. As pointed out by Nast and Bailey (1946), scalariform pitting tends to predominate in the *inner* rings of the stem wood of *Euptelea*, while opposite-multiseriate pitting is characteristic of the larger vessels in the *outer* rings of the older stemwood. However, vessels with scalariform pit pairs occasionally occur in the old wood of *E. pleiosperma*. Phylogenetically, opposite intervacular pitting is reasonably to be interpreted as evolutionarily more advanced than is scalariform pitting among woody angiosperms. In this respect the fossil species is less highly specialized than the two living species of *Euptelea*.

In the proposed new species of *Euptelea* the perforation plates of the vessel elements, however, commonly exhibit a more specialized structure than those of the two living forms. Both *E. polyandra* and *E. pleiosperma* are characterized in the mature secondary xylem by numerous fine bars (20–90) in their vessel perforation plates. The vessel perforation plates of *E. baileyana* usually possess from 5 to 35 bars, most frequently about 15. Also, in contrast to the living species the individual bars are more widely spaced (PLATE III, FIG. 2).

Very little wood parenchyma is present in the fossil *Euptelea* and its presence can be detected only because of the unusual degree of structural preservation. In living species of *Euptelea*, the wood parenchyma is distributed apotracheally and varies from fairly abundant to extremely scanty. In the range of material examined in this study it was observed that wood parenchyma is less abundant in *E. pleiosperma* than in *E. polyandra*. Terminal parenchyma, noted by Metcalfe and Chalk (1950), was not observed. The apparent extreme paucity of wood parenchyma in the fossil may be explained by a variety of factors. One of these is the difficulty of distinguishing between the effect produced by the loss of cell wall substance from the secondary walls of the tracheary elements and the true thin secondary wall and correspondingly larger lumen of parenchymatous elements. Owing to the differential rate of degradation of the various lamellae of the secondary wall various histological effects are produced in fossil plant residues which must be interpreted with this factor in view (Barghoorn 1952).

The largest ray observed in our thin sections of *Euptelea baileyana* is 18 cells in width. In *E. pleiosperma*, which has wider rays than *E. polyandra*, the largest ray observed was 13 cells in width. This is not a large

quantitative difference with respect to this structural feature in comparing the living and fossil species. The frequency of broad, multiseriate rays in the fossil wood, however, is considerably greater than that occurring in either of the two extant species of *Euptelea*. The material of *E. pleiosperma* examined, however, does not represent wood of ring development directly comparable with that of the fossil, being from wood formed in more central rings. Inasmuch as there is a marked increase in ray width during ontogeny of the woody cylinder (Barghoorn 1940) it would be desirable to compare ray width from rings of comparable radii. Wood from the outer rings of large stems of *E. pleiosperma* might show the presence of a higher proportion of large multiseriate rays. Unfortunately, material for determining this feature has not been available.

The close agreement in major diagnostic features as well as in numerous microscopic details of anatomical structure provides convincing evidence that the Clarno fossil wood is closely related to *Euptelea*. Determination of the degree of relationship necessitates careful evaluation of the three observable differences between the Eocene and the modern wood. These differences are limited to 1) the nature of the intervacular pitting, 2) the fine structure of the vessel end walls and perforation plates and 3) the proportion and size of the broad multiseriate rays. In each of these categories, the range of structural variation between the living species of *Euptelea* and the proposed fossil species is less than that which may be found, in numerous instances, among species of a single living genus. For example in *Magnolia* and *Carpinus*, among other genera, the vessel perforation plates vary from scalariform to simple. In *Platanus* and in many genera of the Lauraceae, as examples which may be drawn from a wide range of the dicotyledons, both scalariform and simple perforation plates may be observed in a single radial section. Phylogenetically, these structural differences are more quantitative than qualitative, and in our interpretation of the fossil wood we are extending the morphological range of *Euptelea* rather than proposing a new generic category of the Eupteleaceae.

It has been noted that the vessel perforation plates in the fossil *Euptelea* are more highly specialized than those of the living species of the genus, whereas the intervacular pitting gives evidence of a lesser degree of specialization. This apparent contradiction, however, does not seriously prejudice our assignment of the fossil form to *Euptelea*. Rather, it illustrates the observations of Bailey (1944), drawn from comparative study of the woods of the dicotyledons as a whole, viz., that the phylogenetic modifications of structural features of the vessels of the dicotyledons proceeded at more or less independent rates.

On the basis of close agreement in wood structure the Clarno fossil wood is assignable to the genus *Euptelea*. This genus occupies an isolated position, taxonomically, and possesses secondary xylem of characteristic structure. The possibility that a comparable combination of structural features has arisen quite independently in other families of the more primitive angiosperms seems extremely remote, although this possibility has been considered. Our species has been placed in an extant genus since in our

opinion no useful purpose would be served by clouding its affinities through appending “-oxylon” to its generic name.

The occurrence of *Euptelea* as a component of the early Tertiary forests of western United States strengthens the growing evidence that our early Cenozoic floras show stronger affinities to the woody flora now occupying southeastern Asia than has been generally recognized. It serves also to demonstrate the extreme complexity in generic composition of the early Tertiary floras and the difficulties inherent in interpreting them in terms of present day distributional patterns and associations of woody plants.

SUMMARY

A specimen of silicified wood from the Eocene Clarno formation of north central Oregon has been identified as an extinct species of the Asiatic genus *Euptelea*. The wood differs from that of the two living species in only three minor structural details: 1) character of the pitting of the vessel walls; 2) fine structure of the scalariform perforation plates of the vessel end walls; 3) occurrence of a larger proportion of broad multiseriate rays. These differences are quantitative and not qualitative in the evolutionary specialization of secondary xylem; the authors regard them as extending the morphological range of the genus rather than the basis for proposing a new genus. Accordingly, the specimen has been designated as an extinct species of *Euptelea*, *E. baileyana*. This represents the first fossil record of the genus and establishes its former existence in North America.

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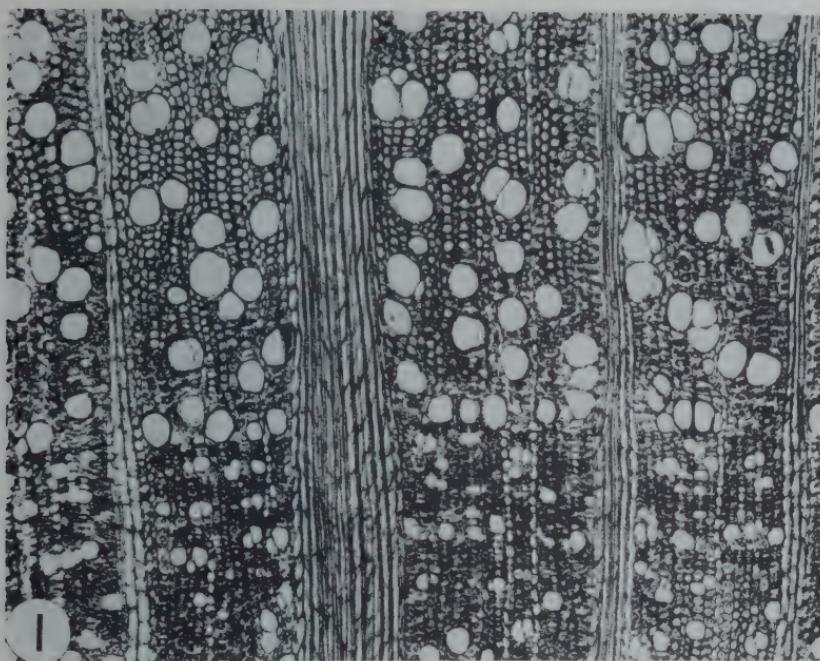
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EXPLANATION OF PLATES

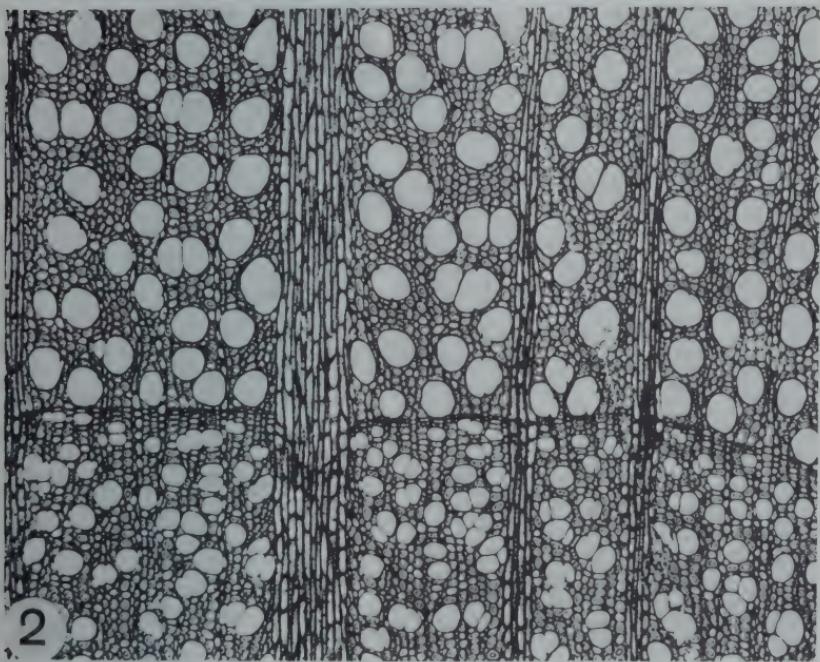
PLATE I. FIG. 1. *Euptelea baileyana* Scott & Barghoorn sp. nov. Transverse section of the wood. $\times 50$. Note the close agreement in major structural features to the modern wood shown below. FIG. 2. *E. pleiosperma* Hook. f. & Thoms. Transverse section of the wood. $\times 50$.

PLATE II. FIG. 1. *Euptelea baileyana*. Tangential section of the wood. $\times 50$. Note the larger proportion of broad multiseriate rays than in the modern wood shown below. FIG. 2. *E. pleiosperma*. Tangential section of the wood. $\times 50$.

PLATE III. FIG. 1. *Euptelea baileyana*. Radial section of the wood. $\times 50$. Note the numerous thin walled tyloses in the vessels. FIG. 2. *E. baileyana*. Radial section of the wood showing scalariform perforation plates. $\times 250$. FIG. 3. *E. baileyana*. Radial section of the wood showing scalariform intervacular pitting. $\times 250$.



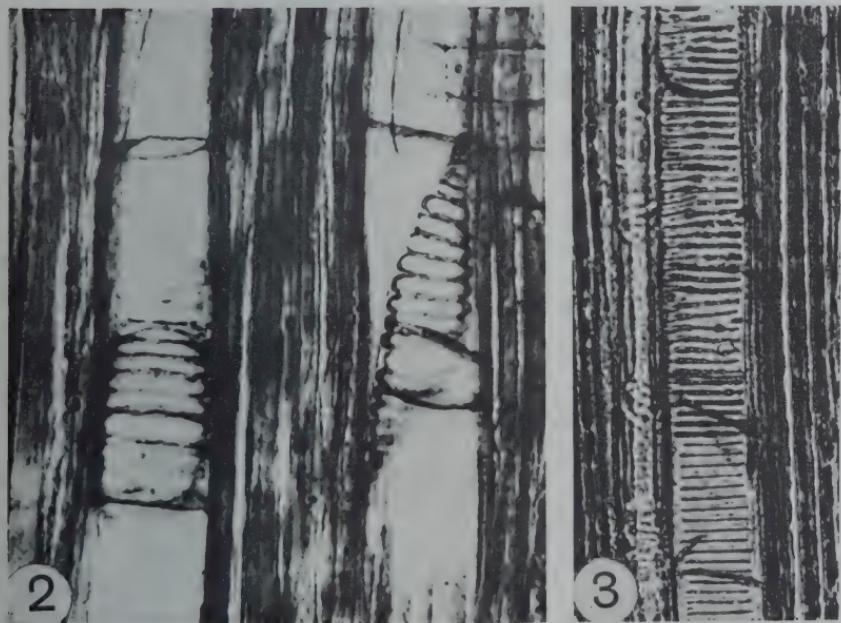
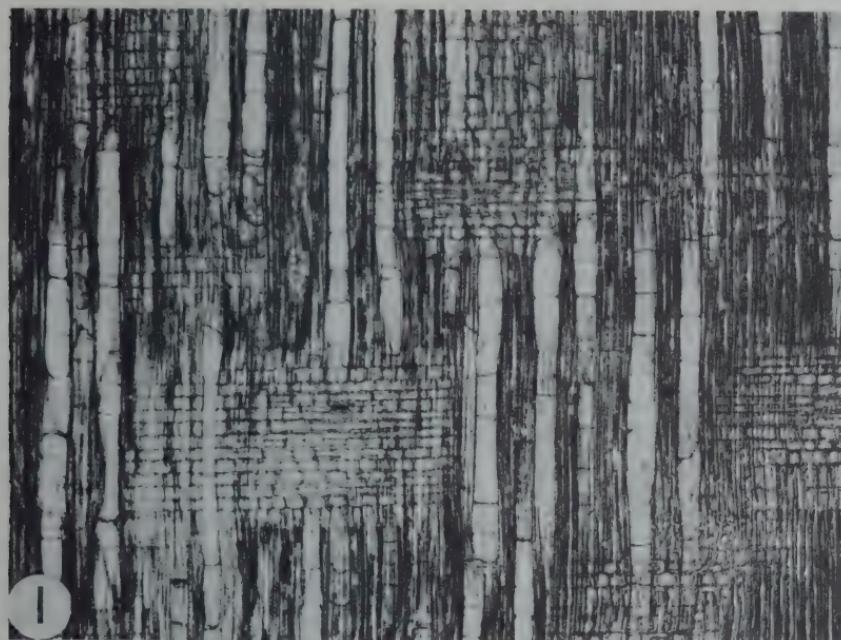
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SCOTT AND BARGHOORN, EUPTELEA IN THE CENOZOIC





SCOTT AND BARGHOORN, EUPTELEA IN THE CENOZOIC

STALK DIAMETER AS A FACTOR IN FRUIT SIZE

EDMUND W. SINNOTT

Among those factors determining the size to which a fruit will grow, the diameter of its stalk or pedicel should evidently be considered, for through this structure must pass all the material of which the fruit is composed. In the author's cultures of *Cucurbita pepo* there are genetic races differing greatly in fruit size, ranging from types derived from the Connecticut field pumpkin (Line CF) with a fruit diameter of about 300 mm. to small, roundish gourds of about 50 mm. (Line SRC). The purpose of the present study is to determine whether there is any relation in these races between the stalk diameter and the size of their fruits.

In small races like SRC the stalks are about 5 mm. in diameter at maturity and in large ones like CF, about 20 mm. The ratio of fruit diameter to stalk diameter is therefore not very greatly different in the two types. The ratio of fruit *volume* to cross sectional area of stalk, however, is obviously far greater in the larger types than in the small, the former having about 14 times as much fruit volume per unit cross section of stalk as the latter. On the basis of these figures, stalk diameter would therefore seem to have little limiting effect on the attainment of fruit size. It is obvious that the flow of material through the stalk must be very much faster in the large races. It should be remembered, however, that it takes much longer for the fruit of the large race to reach full size than for that of the small, so that more time is available to deliver material to the growing fruit.

In an attempt to gain more information on this problem, two methods of attack were undertaken: a study of the relative growth rate of stalk to fruit in large-fruited and small-fruited races, and a study of growth rate and fruit size in developing fruits of both types where the cross-sectional area of the stalk was experimentally reduced.

GROWTH STUDIES

Daily caliper measurements were made of stalk diameter and of ovary length and width in more than 50 normally growing ovaries belonging to eight races of *C. pepo* ranging in mature fruit size from a volume of about 60 cc. to one of 10,000 cc. Readings were made to tenths of a millimeter on stalk diameter and small ovary dimensions, and to the nearest millimeter on larger ones. They were begun with the smallest ovary primordia that could be measured without injury, usually about five to eight days before the opening of the flower, and were continued until growth ceased. This study was made on field-grown plants at the peak of their development, during the last two weeks of July and the first two of August.

The relation between fruit size and the rate and duration of growth in this material has previously been described by the author (1945). From the beginning of development until about three to ten days after flowering (depending on the race) growth is exponential, and the logarithms of the dimensions, when plotted against time, fall along an essentially straight line. Growth rate then falls off gradually until it ceases altogether. *Rate*

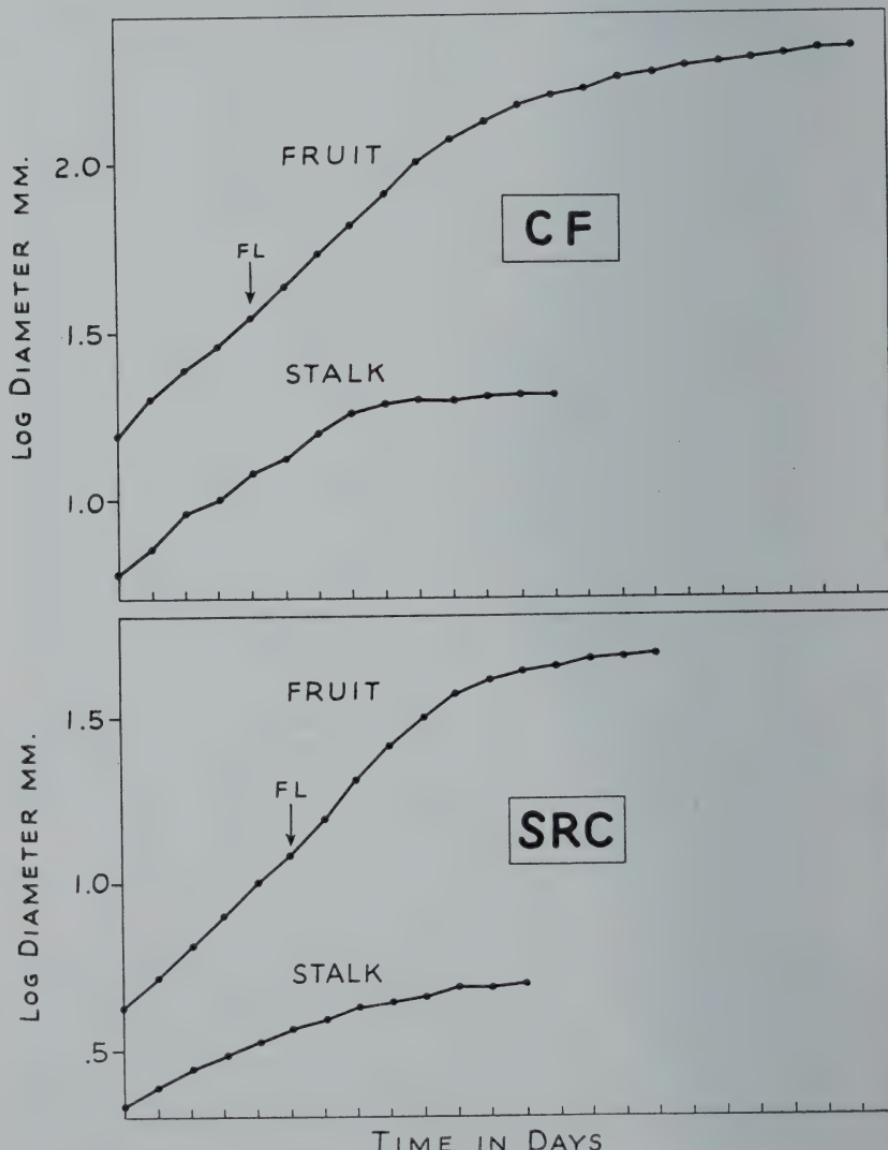


FIG. 1. Growth curves, in days, of the logarithms of diameter of stalk and of fruit in a typical example of a large-fruited line (CF) and of a small-fruited line (SRC). FL marks the day when the flower opened.

of growth during the exponential period is approximately the same in large-fruited and in small-fruited types. The *duration* of both phases of growth, however, is considerably larger in the large-fruited races, and it is to this that the size differences in the mature fruit are due. Typical growth curves for a fruit of a large and of a small race are shown in FIG. 1.

Growth of the stalk in diameter follows the same program as of the ovary, with an early exponential phase succeeded by a gradual diminution until growth ceases. Stalk growth differs in two respects, however, from that of fruit: its exponential growth rate is lower, and its growth ceases much earlier, when the fruit is only one-fourth of its final size or less. These relations are also shown in FIG. 1. As a result, the differential in size between fruit diameter and stalk diameter, which at the beginning is not very great, continually increases.

Between the large and the small races there are differences in these growth relationships. In the large ones the exponential growth rate of the stalk is considerably higher than in the small. In a typical growth curve of the line CF, for example, it is about 16% per day, but in line SRC only 10%. These rates compare with about 22% for daily fruit growth in both. The relative growth of stalk to fruit is thus related to the typical fruit size at maturity. The relative-growth constant of stalk diameter to fruit diameter was determined in the usual manner for six races and is shown in TABLE 1, together with the typical mature fruit volume of each race.

TABLE 1

Line	Volume of typical mature fruit in cc	Constant of relative growth (<i>k</i>) of stalk diameter to fruit diameter
CF	10,000	.69
P	2,500	.62
AC	680	.65
HG	290	.63
TA	70	.48
SRC	60	.48

At two points on the growth curve there is a relationship between stalk growth and fruit growth in all races which may have morphogenetic significance. One is at the time of flowering. The proportional logarithmic difference between stalk and fruit diameter steadily increases and in both large and small types, when this difference reaches about 5 or 6 logarithmic units, flowering occurs. In other words, the flower opens when the diameter of the young fruit has reached about three to four times that of the stalk. This is quite independent of the absolute size of either. Since the stalk grows faster in large types than in small, it takes longer in them for this absolute differential to be reached, and thus both ovary and stalk are considerably larger at flowering than they are in small types.

The fact is also evident, whatever its significance, that the end of ex-

ponential fruit growth coincides with the end of growth in stalk diameter. Thus all the post-exponential growth of the fruit, during which its volume increases four-fold or more, takes place after the stalk has reached its full size.

EXPERIMENTS

To determine whether the diameter of the stalk actually influences the size to which the fruit will grow, this diameter was experimentally reduced in growing fruits of both large and small types.

In one series this was done by half severing the young stalk by cutting a deep nick out of its side as far as the center of the pith, so that only half of the normal area of the stalk was available for transport of material from plant to fruit. The operation was performed on the day of flowering, or near it. About half the operated flowers stopped growing in a day or two and died, apparently because the cut was too deep, too much sap was lost, or infection set in. In ten fruits, belonging to four lines and differing widely in their normal fruit size, however, active growth continued. The cut surfaces healed well and although considerable scar tissue was formed, vascular connection across the gap was not restored. Daily caliper measurements of ovary width were made on these fruits. In every case where growth continued after the operation it proceeded at the normal rate, and growth curves for these fruits are not different in any notable way from those for intact ones.

Stalk diameter was also reduced by artificially constricting the stalk early in development and thus preventing its growth. Attempts to do this by embedding the stalk in plaster of Paris failed, for the plaster was soon cracked by stalk growth. Constriction was successfully accomplished by winding coarse, soft cotton string around the stalk, firmly but not too tightly, for a length of from several millimeters to a centimeter. In some of the stalks thus bound the string was reinforced by a layer of plaster. Binding was usually done on the day of flowering or shortly thereafter. Young ovaries from six lines were thus constricted.

Many of these failed to grow and died in a few days. Twenty-three continued to develop, however, and width measurements on them were made daily. Growth curves of such fruits, from both large and small races, were essentially normal as to rate and total final size.

After growth had ceased, the stalks were freed and examined. In every case it was found that growth had either been greatly reduced or had not taken place at all after binding. The tissues of the stalk were poorly developed and the vessels were much narrower than in normal stalks. Diameter of the stalk above and below the constriction was a little affected.

DISCUSSION

Experimental evidence shows that a stalk very much smaller in cross section than normal, either because of the removal of part of it or the prevention of its growth, will nevertheless conduct material from plant to

fruit as rapidly and to as large a final amount as a stalk of normal diameter. This confirms the results of some other workers, notably Werner (1931). He found after cutting off all the roots of a maize plant except one small prop root and thus reducing the amount of vascular connection between soil and plant to about one thousandth of its normal cross-sectional area, that the plant grew almost as well as the controls and the amount of transpiration was essentially normal.

Other evidence has shown that the volume of the transpiration stream conducted through a young stem is not related to the amount of xylem which is developed there; in other words that "functional stimulus" of a tissue does not result in its greater development. This is what we should expect from a study of anatomical evidence. In *Osmunda*, for example, the cross sectional area of the xylem of a leaf trace as it leaves the stele is only about $\frac{1}{8}$ that which it attains in the rachis above, but this small bundle conducts all the water that the large one does. The large and complex vascular system of a cycad leaf, also, is connected with the vascular axis of the stem by only two small bundles. Evidently in such cases, including the ones here described, the conducting capacity of a structure is considerably higher than it is normally called upon to display, and increased demands upon it do not increase its size.

The close relationship between stalk growth and fruit growth in the material here described, however, and especially the difference in growth patterns between large-fruited and small-fruited types suggests that there may be a correlative growth influence between stalk and fruit which is not related merely to transport of material. The fact that stalk diameter grows more slowly than fruit diameter necessarily results in an increasing tension, so to speak, between the two which might be expected ultimately to affect fruit growth. The further fact that when this growth differential reaches a certain absolute size, flowering takes place in both large and small types, suggests that this differential is in some way related to the attainment of sexual maturity. As the difference grows still greater, another change — the cessation of exponential growth in the fruit — occurs, again suggesting that there is a correlative influence of stalk on fruit. What the physical basis of this correlation may be is unknown. It would be interesting to study the auxin relationships between stalk tissue and ovary tissue in these plants.

We may conclude that there is a definite relation between the relative-growth pattern of the stalk and the fruit in *Cucurbita pepo*, but that the size of the fruit does not depend directly on the cross-sectional area of its stalk.

SUMMARY

Diameters of developing fruits and fruit stalks were measured daily in races of *Cucurbita pepo* differing widely in mature fruit size.

Growth of the stalk is slower and ceases earlier in small-fruited races than in large-fruited ones.

In both, flowering occurs when the ratio of ovary diameter to stalk diameter has reached a specific size.

Artificial reduction of stalk diameter by cutting away part of it or by constricting it had no appreciable effect on fruit growth.

Size of fruit does not depend on cross-sectional area of the stalk but there seems to be a correlation between the growth pattern of the stalk and that of the fruit, which is related to fruit size.

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PHANEROGAM GENERA WITH DISTRIBUTIONS TERMINATING IN FIJI

A. C. SMITH

PROFESSOR I. W. BAILEY (1) has aptly commented on the significance of the Indo-Malaysian region in studies of angiosperm phylogenies. The area delineated by him extends to the southeast as far as New Caledonia and Fiji. In view of the supposed geological boundary of an old Melanesian continent in Fiji (2, 4, 5, 6, 7, 9), as indicated by the occurrence there of continental rock formations, we may well consider whether this region is critical as the terminating point of a significant number of plant groups. An examination of relevant data at the species level would not be very revealing, since in Fiji about 70 percent of the phanerogam species are endemic, while a large proportion of the remaining species have such wide distributions and such efficient means of dispersal that their existing ranges are not enlightening. At the generic level, however, it is possible that the pertinent data will aid in answering the central question, namely whether or not a significant distributional break occurs in or east of Fiji and coincides with the putative boundary between the continental and the oceanic archipelagos. I have already touched on this problem (8), and the present notes are intended as documentation of the conclusions there suggested.

It would perhaps have been advisable to consider the Fiji-Tonga region as a unit, since Tonga is also sometimes supposed to have been marginal on the old continent. The botanical evidence, too, points to a fundamental similarity between the Tongan and Fijian floras, the former being in effect an attenuation of the latter, with very few supplementary taxa at the generic level. The list of genera discussed in this paper would have been somewhat longer if Fiji and Tonga could have been treated together, since several, or perhaps many, genera have ranges terminating in Tonga and therefore omitted from consideration here. A more natural geological boundary would have been the sea between Fiji-Tonga to the west and Samoa to the east, and I believe that the botanical evidence will corroborate this. However, no dependable catalog of the Tongan phanerogam flora is available, whereas an accumulation of notes toward my proposed Flora of Fiji gives me a reasonably complete picture of what phanerogams are now known to occur in Fiji. In the preparation of this paper I have utilized the card-catalog of Polynesian references compiled by Dr. E. D. Merrill, now in the library of the Arnold Arboretum of Harvard University, and have consulted whatever recent revisions are available as well as the herbaria at Harvard and the U. S. National Museum.

There follow, arranged essentially in the Dalla Torre & Harms sequence, discussions of the phanerogam genera that occur indigenously in Fiji but are not found in the island groups farther east. A concluding tabulation and discussion summarize the data.

PODOCARPACEAE

Dacrydium Soland. Pilger (in E. & P. Nat. Pfl. ed. 2. 13: 239. 1926) mentions *Dacrydium* as a genus of about 20 species; except for one species in southern Chile, its range is Indo-Malaysian. It extends eastward to New Guinea, New Caledonia, New Zealand, and Fiji, where the widespread *D. elatum* (Roxb.) Wall. and the New Caledonian *D. lycopodioides* Brongn. & Gris have been recorded.

Acmopyle Pilger. This small genus is known from two species in New Caledonia and a single endemic species in Fiji, *A. sahniana* Buchholz & Gray (in Jour. Arnold Arb. 28: 142. 1947).

ARAUCARIACEAE

Agathis Salisb. This genus, with 20 or more species, is distributed from the Malay Peninsula through Malaysia to Australia, New Zealand, New Caledonia, the New Hebrides, and Fiji, where the endemic *A. vitiensis* (Seem.) Drake terminates its range.

TRIURIDACEAE

Andruris Schlechter. In his recent treatment of the Triuridaceae, Giesen (in Pflanzenr. 104 [IV. 18]: 15-29. 1938) recognizes 15 species of *Andruris*, which extends from southeastern Asia and Japan to Micronesia, New Guinea, and Queensland, with the outlying endemic *A. vitiensis* (A. C. Sm.) Giesen in Fiji. The genus does not occur in the islands between Fiji and the New Guinea-Queensland region, but the related *Sciaphila* is in New Caledonia and the New Hebrides.

PALMAE¹

Calamus L. This vast genus, according to Beccari's revision in Ann. Bot. Gard. Calcutta 11 (1): 1-510. 1908, is distributed from Africa and southeastern Asia through Malaysia to New Guinea and Fiji, where the endemic *C. vitiensis* Warb. terminates its range. More recently the genus has been reported from the New Hebrides.

Neoveitchia Becc. Beccari (in Webbia 5: 76-79. 1921), realizing that Wendland's genus *Veitchia* (in Seem. Fl. Vit. 270. 1868) included two elements, established the genus *Neoveitchia* for *V. storckii*, leaving *Veitchia* for Wendland's remaining three species and three additional new ones. *Neoveitchia*, in the sense of *N. storckii* (H. Wendl.) Becc., remains a monotypic endemic Fijian genus.

Unfortunately, *Veitchia storckii* is listed as the type species of the conserved generic name *Veitchia* (Internat. Code Bot. Nomencl. 89. 1952). The intention in conserving *Veitchia* H. Wendl. (1868) over *Veitchia* Lindl. (1861) was doubtless to conserve it in the sense of the familiar

¹ The data upon which this discussion of the palms is based were kindly supplied by Dr. Harold E. Moore, Jr., of the Bailey Hortorium.

V. joannis and its immediate relatives. Beccari's prior removal of *V. storckii* from *Veitchia* was apparently overlooked when this species was listed as the genotype. Nevertheless, conservation in this sense is binding until revised, thus leaving *V. joannis* without a valid generic name. In the present treatment we disregard the Code's listing of a type species and return to Beccari's arrangement; a formal proposal to this effect will be made to the next International Congress.

Veitchia H. Wendl. As noted above, we here discuss *Veitchia* in Beccari's sense, as including *V. joannis* H. Wendl. and its immediate relatives, an interpretation that preserves current usage. In this sense, *Veitchia* consists of approximately nine species, of which three are endemic to Fiji. Otherwise there are three or four in the New Hebrides and one in New Caledonia, all endemic, and one known only from cultivated material. *Neoveitchia storckii* (H. Wendl.) Becc. is not a close relative of this group of species.

Vitiphoenix Becc. This endemic genus is represented by eight Fijian species, some being transfers from *Ptychosperma* (Burret in Rep. Sp. Nov. 24: 282-285. 1928) and others more recently described (Burret in Bishop Mus. Occ. Pap. 11 (4): 7-10. 1935; A. C. Sm. in Jour. Arnold Arb. 31: 145. 1950). The genus is very closely allied to *Veitchia* H. Wendl. (in the sense used above) and may eventually have to be combined with it.

Exorrhiza Becc. *Exorrhiza* should probably be included in this treatment, on the basis of Burret's discussion in Notizbl. Bot. Gart. Berlin 12: 591-593. 1935. It is definitely known to include four species, of which three are endemic to Fiji and one to the New Hebrides. A fifth species, *E. vaupelii* Burret, of Samoa, is inadequately known and is suspected by Burret to belong in *Clinostigma*. The relationship of *Exorrhiza* seems to be with *Bentinckia* Becc.

Goniosperma Burret. This endemic genus has two species in Fiji, *G. vitiense* Burret and *G. thurstonii* (Becc.) Burret (in Bishop Mus. Occ. Pap. 11 (4): 10-12. 1935). *Goniosperma* belongs to a group of small, often monotypic, genera extending throughout much of Melanesia, Polynesia, and Micronesia, but apparently absent from the larger islands such as New Guinea. A close relative of *Goniosperma* may be the New Caledonian *Cyphosperma* H. Wendl. rather than *Physokentia* Becc., with which Burret compared it.

Taveunia Burret. This apparently rare endemic genus is known from a single Fijian species, *T. trichospadix* Burret (in Bishop Mus. Occ. Pap. 11 (4): 12-14. 1935). Its relationship, in general, is with the cyphospermate palms.

Goniocladus Burret. This endemic genus is represented by a single Fijian species, *G. petiolatus* Burret (in Notizbl. Bot. Gart. Berlin 15: 87. 1940). *Goniocladus* is another little-known genus that cannot be accurately related at present, beyond placing it among the cyphospermate palms.

ORCHIDACEAE²

Cryptostylis R. Br. *Cryptostylis*, a genus of 25 or more species, extends from Ceylon through Malaysia and the Philippines to New Guinea and Australia, with one outlying endemic species in Fiji, *C. vitiensis* Schlechter.

Chrysoglossum Bl. This genus of about 15 species ranges from the Himalayas and southern China through Malaysia and the Philippines to New Caledonia, the New Hebrides, and Fiji, being represented in the last archipelago by three species, of which two (*C. gibbsiae* Rolfe and *C. vesicatum* Reichb. f.) are endemic.

Acanthophippium Bl. This small genus of ten species extends from India and southern China through Malaysia and the Philippines to New Guinea, with a single endemic outlying species in Fiji, *A. vitiense* L. O. Williams (in Am. Orch. Soc. Bull. 10: 169. 1941). The archipelagos between New Guinea and Fiji have not yet disclosed the genus.

Eulophia R. Br. *Eulophia*, a genus of about 200 species, is most abundant in Africa, but it also has a wide distribution in America, Australia, southeastern Asia, and Malaysia, continuing eastward to Micronesia, New Caledonia, the New Hebrides, and Fiji, where its range is terminated by two species, neither endemic.

Grammatophyllum Bl. This small genus, of seven species, occurs through Malaysia and the Philippines, extending eastward to the Solomon Islands and Fiji, where it is represented by the endemic *G. elegans* Reichb. f.

Sarcanthus Lindl. *Sarcanthus*, with 75 or more species, ranges from southeastern Asia through Malaysia and the Philippines to Micronesia and New Guinea, with the outlying endemic *S. nagarensis* Reichb. f. in Fiji. I do not find records of the genus in the groups between New Guinea and Fiji.

Chroniochilus J. J. Sm. Only two widely separated species are known of this little genus, *C. minimus* (Bl.) J. J. Sm., of Java, and the Fijian endemic *C. godeffroyanus* (Reichb. f.) L. O. Williams. This peculiar disjunct distribution indicates that the generic disposition of species from the intervening regions should be checked; a somewhat similar case is found in the little genus *Calyptosepalum* (cf. Santalaceae).

BALANOPSIDACEAE

Balanops Baill. The single genus of the Balanopsidaceae has a narrow distribution, from Queensland to New Caledonia, the New Hebrides, and

² I am greatly indebted to Dr. Richard E. Schultes and Mr. Charles Schweinfurth, of the Ames Orchid Herbarium, Harvard University, for checking these records of Orchidaceae.

Fiji. The variability of the one Fijian species, *B. vitiensis* (A. C. Sm.) Hjelmqvist, was discussed by me in *Jour. Arnold Arb.* 31: 149-150. 1950.

PROTEACEAE

Kermadecia Brongn. & Gris. This small genus has a very compact range, with seven species in New Caledonia (Guillaumin, *Fl. Nouv.-Calédon.* 108. 1948), one in Queensland, one in the New Hebrides, and two endemic Fijian species, *K. vitiensis* Turrill and *K. ferruginea* A. C. Sm., terminating its range to the east.

SANTALACEAE

Calyptosepalum S. Moore. That *Calyptosepalum* does not belong in the Santalaceae, where it was placed by Moore, has been pointed out by I. W. Bailey and A. C. Smith (in *Jour. Arnold Arb.* 34: 52-64. 1953); we suspect it to represent an independent family, as yet unproposed, but for purposes of the present mention I list it where originally described. The distribution of the two known species of *Calyptosepalum* raises many questions. The original Sumatran species, *C. sumatranum* S. Moore, appears to be very rare, and the second species, *C. pacificum* I. W. Bailey & A. C. Sm., is a Fijian endemic known only from the type collection.

AMARANTHACEAE

Deeringia R. Br. The genus reaches its southeastern limit in Fiji, where it is represented by *D. amaranthoides* (Lam.) Merr., widely distributed from continental Asia through Malaysia and Australia to Micronesia and Fiji.

RANUNCULACEAE

Clematis L. This large and widespread genus, probably with more than 200 species, occurs in Australasian regions as far east as New Caledonia and Fiji, but I find no records of it in Polynesia. Kuntze (in *Verh. Bot. Ver. Brand.* 26: 83-202. 1885) does not mention any distribution of the genus beyond Fiji in the Pacific. The Fijian species, *C. pickeringii* A. Gray, has been attributed a range including New Caledonia, New Guinea, and even Australia by some authors; Kuntze treats this taxon as *C. aristata* var. *pickeringii* (A. Gray) Kuntze.

MENISPERMACEAE

Pachygone Miers. Diels (in *Pflanzenr.* 46 [IV. 94]: 241-246. 1910) recognizes 11 species of *Pachygone*, but several have since been added. The genus occurs from India and southern China to Micronesia, New Guinea, northern Australia, and New Caledonia, with a single terminating endemic species, *P. vitiensis* Diels, in Fiji. I find no report of the genus from the Solomons or the New Hebrides.

DEGENERIACEAE

Degeneria I. W. Bailey & A. C. Sm. This monotypic genus, the basis of an endemic family related to the Magnoliaceae and Himantandraceae,

has been discussed at some length (in *Jour. Arnold Arb.* 23: 356-365. 1942, 30: 1-38. 1949).

ANNONACEAE

Desmos Lour. This essentially Indo-Malaysian genus is known in Fiji from *D. insularis* and *D. leucanthus*, endemic species described by the writer, although otherwise it appears not to have been reported east of the Philippines.

Polyalthia Bl. Nine endemic Fijian species mark the eastern boundary of this large genus, which ranges from Africa and Asia to Australia and Melanesia. It should be noted, however, that the probable occurrence of the genus in Tonga is indicated by one of Professor T. G. Yuncker's recent collections, although works on the plants of Tonga do not list it. This would be an expected continuation of the range, especially since one of the Fijian species is known from southern Lau.

Xylopia L. This large genus, occurring in tropical regions in America, Africa, and Asia, extends in Melanesia as far as Fiji, where three endemic species described by the writer terminate its range to the east.

Cyathocalyx Champion. Four endemic Fijian species described by me (cf. *Jour. Arnold Arb.* 31: 160-164. 1950) mark the eastern boundary of this Indo-Malaysian genus.

Richella A. Gray. This is apparently the correct generic name for the large genus currently passing as *Oxymitra* Hook. f. & Thoms. Its extensive Indo-Malaysian and African distribution extends in Melanesia to New Caledonia and Fiji, in which latter group it ends in the endemic *R. monosperma* A. Gray, the type of the genus. The 1954 International Congress did not accept my proposal to conserve *Oxymitra* (1855) in the sense of the annonaceous genus (cf. *Taxon* 3: 115. 1954), and so *Richella* (1852) must be used as the correct name for this concept, if the view prevails that the two taxa are congeneric (cf. A. C. Sm. in *Bishop Mus. Bull.* 141: 62. 1936). In this case the name *Friesodielsia* van Steenis (in *Bull. Bot. Gard. Buitenz.* III. 17: 458. 1948) will not be necessary and approximately 80 new combinations under *Richella*, thus far applied only to the Fijian species, will be needed.

CUNONIACEAE

Geissois Labill. The range of *Geissois* centers in New Caledonia, but some of its approximately 17 species occur in Australia, the New Hebrides, and Fiji. In the latter archipelago four endemic species are known (cf. A. C. Sm. in *Jour. Arnold Arb.* 33: 120-128. 1952).

Pullea Schlechter. Eight species are known in *Pullea*, six of them in New Guinea (cf. Perry in *Jour. Arnold Arb.* 30: 163-165. 1949), one in Queensland, and one, *P. perryana* A. C. Sm. (in op. cit. 33: 148. 1952), in Fiji. The genus is as yet unreported from the Solomons or the New Hebrides.

CONNARACEAE

Connarus L. *Connarus* has a tricentric distribution in America, Africa, and Asia, from which it extends eastward through Malaysia as far as Fiji; here it ends in the endemic *C. pickeringii* A. Gray.

LEGUMINOSAE

Parkia R. Br. *Parkia*, a genus of 30 or more species, occurs in tropical America, Africa, and the southeastern Asia-Malaysia region. Although a species is recorded from Micronesia, there is a wide distributional gap east of the large Malaysian islands to Fiji, where *P. parrii* Horne ex Baker terminates its range.

Cynometra L. The 60 or more species of *Cynometra* are found in tropical America and Africa, as well as in southeastern Asia, Malaysia, and Micronesia. One species is recorded from New Caledonia and two from Fiji, *C. falcata* A. Gray and *C. insularis* A. C. Sm., terminating the generic range.

Kingiodendron Harms. The very scattered distribution of the four species of *Kingiodendron* has been discussed by Burtt (in Kew Bull. 1936: 461. 1936). The species, of very local range, occur in southern India, the Philippines and New Guinea (cf. Merrill & Perry in Jour. Arnold Arb. 23: 399. 1942), the Solomon Islands, and Fiji, where *K. platycarpum* Burtt is the most easterly species.

Storckia Seem. This little genus is represented by two New Caledonian species and by *S. vitiensis* Seem. The last has been considered endemic to Fiji, but Guillaumin (Fl. Nouv.-Caléd. 156. 1948) lists it from New Caledonia, without documentation.

LINACEAE

Durandea Planch. This genus of 13 species, according to Staph (in Hook. Ic. Pl. 29: tab. 2822. 1906), has a range of Borneo, New Guinea, and Queensland to the Solomon Islands and New Caledonia, with a single outlying endemic species, *D. vitiensis* Staph, in Fiji.

RUTACEAE

Wenzelia Merr. In his treatment of the subfamily Aurantioideae, Swingle (in Webber & Batchelor, Citrus Industry 1: 129-474. 1943) discusses *Wenzelia* as having nine species, distributed 1 in the Philippines, 6 in New Guinea, 1 in the Solomon Islands, and 1 in Fiji. The endemic Fijian species, *W. kambarae* Swingle, is known only from the Lau group.

SIMAROUBACEAE

Amaroria A. Gray. This endemic monotypic genus is known only from *A. soulameoides* A. Gray, one of the most abundant small trees in the Fijian forests. The genus is placed by Engler (in E. & P. Nat. Pfl. ed. 2. 19a: 393-394. 1931) as one of three genera in the tribe Soulameae.

Engler (loc. cit.) also mentions the related genus *Soulamea* Lam. as occurring in Fiji; its stated range extends from the Seychelles through Malaysia to Micronesia, New Guinea, New Caledonia, and Fiji, where the widespread *S. amara* Lam. is said to occur. I have seen no other reports of the occurrence of *Soulamea* in Fiji, nor are any herbarium records available to me. Therefore, until this occurrence is further verified, I think that a misidentification was probable. The two species concerned are superficially rather similar, but differences in flowers and fruits, as outlined by Engler, appear to be of generic significance.

Another simaroubaceous genus indicated as terminating in Fiji is *Brucea* J. F. Mill., this record being based on *B. quercifolia* Seem., a supposed endemic. This species is not mentioned by Engler (in op. cit. 386-387. 1931), who indicates the generic range as from tropical Africa through Malaysia and the Philippines to Australia. Without having seen Seemann's type, I am inclined to believe that he had a specimen of *B. javanica* (L.) Merr. (in Jour. Arnold Arb. 9: 3. 1928, a binomial ignored by Engler); both Gillespie and I have collected this species on Taveuni, where it is either cultivated or apparently naturalized. *Brucea*, therefore, may quite confidently be excluded from the indigenous flora of Fiji.

MALPIGHIACEAE

Hiptage Gaertn. Niedenzu (in Pflanzenr. 91 [IV. 141]: 67-84. 1928) recognizes 22 species of *Hiptage*, in addition to four uncertain species, among which is the Fijian *H. myrtifolia* A. Gray. Several species have since been added, the range of the genus being from India, southern China, and Formosa to the Malaysian islands and Fiji, although the outlying *H. myrtifolia* (see Jour. Arnold Arb. 31: 288. 1950, for distribution) is far removed from the remaining species.

EUPHORBIACEAE

Drypetes Vahl. Widespread in the tropics of both hemispheres and represented by at least 160 species (Pax & Hoffm. in E. & P. Nat. Pfl. ed. 2. 19c: 72-73. 1931), *Drypetes* extends into Malaysia and Micronesia, terminating to the southeast in Fiji. Here it is represented by *D. vitiensis* Croizat (in Sargentia 1: 49. 1942), an endemic species which was not further related by its author.

Buraeavia Baill. This small genus is known only from two New Caledonian species and the Fijian endemic *B. horneana* A. C. Sm. (in Jour. Arnold Arb. 33: 374. 1952). Pax & Hoffmann (in op. cit. 75) treat *Buraeavia* as a synonym of *Longetia* Baill., which genus extends westward to the Malay Peninsula but remains very small, with six species according to the Pax & Hoffmann treatment.

Cleistanthus Hook. f. According to Jablonszky (in Pflanzenr. 65 [IV. 147. VIII]: 8-54. 1915), *Cleistanthus* includes at least 106 species and has a range from Africa to Malaysia, Australia, New Caledonia, and Micronesia. In describing the Fijian endemic *C. micranthus*, Croizat ex-

tended the known range to the east and placed his species in the small section *Australes* Jabl., with species only in Queensland and New Caledonia.

Cleidion Bl. A genus of about 20 species, *Cleidion* occurs in tropical America, Africa, and southeastern Asia, with an extension eastward to Micronesia, New Caledonia, and Fiji. In Fiji it is represented by the endemic *C. leptostachyum* (Muell. Arg.) Pax & Hoffm.

Endospermum Benth. *Endospermum*, with at least 15 or 20 species, ranges from southeastern Asia to New Guinea, except for two endemic species in Fiji, *E. macrophyllum* (Muell. Arg.) Pax & Hoffm. and *E. robbieanum* A. C. Sm. Records of the genus in the Solomons, the New Hebrides, or New Caledonia appear to be lacking.

Stillingia Garden ex L. Pax & Hoffmann (in E. & P. Nat. Pfl. ed. 2. 19c: 198. 1931) mention *Stillingia* as including about 30 species, while Rogers (in Ann. Mo. Bot. Gard. 38: 207-259. 1951) recognizes 23 American species. Elsewhere, the genus occurs in Madagascar and Mauritius and has one endemic Fijian species, *S. pacifica* Muell. Arg. This extraordinary generic distribution has been questioned by various students but apparently receives morphological support. Neither the mentioned authors nor Croizat (in Bishop Mus. Occ. Pap. 18: 71. 1944) find any grounds for removal of the Fijian species from the genus.

ANACARDIACEAE

Semecarpus L. f. The genus ranges from continental Asia through Malaysia and into Micronesia, Australia, New Caledonia, the New Hebrides and Fiji, where it is terminated by the endemic *S. vitiensis* (A. Gray) Engl.

CELASTRACEAE

Elaeodendron Jacq. The Indo-Malaysian portion of the range of *Elaeodendron* extends from southeastern Asia and Australia to New Caledonia, the New Hebrides, and Fiji, where it is terminated by the endemic *E. vitiense* A. C. Sm.

HIPPOCRATEACEAE

Salacia L. The genus *Salacia* has about 30 species in America and perhaps as many or more in the Asiatic tropics, where it extends eastward to Micronesia, the New Hebrides, New Caledonia, and Fiji. In the last archipelago it is represented by two endemic species described by me, *S. vitiensis* and *S. pachycarpa*.

SAPINDACEAE

The two genera of Sapindaceae with ranges terminating in Fiji (cf. A. C. Sm. in Jour. Arnold Arb. 31: 299-302. 1950) are remarkable for their disjunct distributions.

Koelreuteria Laxm. This sharply marked genus, with eight species, is limited to eastern Asia and Formosa with the exception of the Fijian

endemic, *K. elegans* (Seem.) A. C. Sm. (in Contr. U. S. Nat. Herb. 30: 518. 1952). Its absence from the intervening areas is puzzling. A somewhat similar, but more extended, type of distribution is noted in *Rhamnella* (Rhamnaceae).

Cossignia Commers. In a different way, the distribution of *Cossignia* is just as puzzling as that of *Koelreuteria*; it is known from four species, of which two are from the Mascarene Islands and one from New Caledonia, the fourth being the recently described Fijian endemic, *C. pacifica* A. C. Sm.

RHAMNACEAE

Ventilago Gaertn. According to Suessenguth (in E. & P. Nat. Pfl. ed. 2. 20d: 151. 1953), *Ventilago*, with about 40 species, ranges from Africa and Madagascar through the Indo-Malaysian region as far east as Micronesia, New Caledonia, and Fiji. In the last archipelago it is represented by the endemic *V. vitiensis* A. Gray.

Smythea Seem. Suessenguth (op. cit. 154) mentions the genus as having about seven species and a range from southeastern Asia through Malaysia to Micronesia, New Guinea, and Fiji; I have found no records of its occurrence farther east. To the species occurring in Fiji, *S. lanceata* (Tul.) Summerhayes, Suessenguth attributes a very wide distribution extending to Micronesia and into Mayalsia as far as Borneo and the Philippines.

The remaining genera of Rhamnaceae that occur in Fiji have ranges extending farther east, but mention should be made of *Dallachya* F. Muell., which Suessenguth (op. cit. 149) maintains as a monotypic genus with a range from Queensland to Fiji. He appears to have overlooked, or to have disagreed with, my reduction of *Dallachya* to *Rhamnella* (in Bull. Torrey Club 70: 544. 1943; cf. also Guillaumin, Fl. Nouv.-Caléd. 203. 1948). At any rate, the species concerned, *Rhamnella vitiensis* (Benth.) A. C. Sm., ranges from Queensland and New Guinea through Fiji to Tonga.

VITACEAE

Cayratia Juss. In his recent treatment, Suessenguth (in E. & P. Nat. Pfl. ed. 2. 20d: 277-282. 1953) accepts about 45 species of *Cayratia*, which is distributed from Africa and southeastern Asia, including Japan, through Malaysia to Micronesia, the Solomon Islands, Australia, New Caledonia, and Fiji. In the last archipelago it is represented by two endemic species, *C. seemanniana* A. C. Sm. and *C. acuminata* (A. Gray) A. C. Sm. (in Sargentia 1: 55-57. 1942). Apparently Suessenguth overlooked my binomials, for he again makes the combination *C. acuminata* and takes the Australian *C. saponaria* (Benth.) Seem. in a very inclusive sense.

Tetrastigma Planch. Suessenguth (in op. cit. 318-329. 1953) mentions *Tetrastigma* as having about 93 species and a range from southeastern Asia through Malaysia to New Guinea and Australia. The genus also occurs in the Solomon Islands (Merr. & Perry in Jour. Arnold Arb. 22: 376. 1941).

and Fiji, where it is represented by the endemic *T. vitiensis* (A. Gray) A. C. Sm. (in Bishop Mus. Bull. 141: 92. 1936). Apparently Suessenguth disagrees with this disposition of *Cissus vitiensis* A. Gray, if this is the implied basionym of his combination *Cayratia vitiensis* (A. Gray) Suesseng. (in op. cit. 281. 1953). Neither this combination nor the above-mentioned *C. acuminata* are validly published by Suessenguth in accordance with Article 42 of the International Code (1952).

TILIACEAE

Berrya Roxb. Burret (in Notizbl. Bot. Gart. Berlin 9: 605–607. 1926) recognizes three species of *Berrya*, extending from southeastern Asia into Malaysia. To these should now be added a New Guinean species (Merr. & Perry in Jour. Arnold Arb. 20: 339. 1939) and the outlying Fijian endemic, *B. pacifica* A. C. Sm. (in Jour. Arnold Arb. 31: 303. 1950).

Microcos L. *Microcos*, a genus of about 75 species, occurs in Africa and more extensively from southeastern Asia into Malaysia as far as New Guinea (cf. Burret in op. cit. 756–796. 1926). A single outlying endemic, *M. vitiensis* A. C. Sm., terminates the range in Fiji, but I find no records of the genus in the New Hebrides or Solomon Islands.

STERCULIACEAE

Pimia Seem. This genus, well enough described and illustrated by Seemann (Fl. Vit. 25. pl. 5. 1865) is too little known for proper evaluation, although such students as Bentham & Hooker and Schumann (in Engler & Prantl) have accepted it as an independent, endemic, monotypic genus. The single species, *P. rhamnoides* Seem., may be known only from the type collection; at least I find no other records in the literature or in herbaria.

Firmiana Marsigli. *Firmiana*, with about 20 known species, has a distribution extending from Africa (west tropical Africa, Tanganyika) to eastern Asia, the Philippines, and Malaysia, where it extends to New Guinea. An outlying Fijian endemic, *F. diversifolia* A. Gray, which is locally quite frequent, terminates the generic range.

Pterocymbium R. Br. This small genus ranges from southeastern Asia into Malaysia; Kostermans (in Reinwardtia 1: 41–49. 1950) has recently discussed the three species occurring in Malaysia. The only record of the genus east of New Guinea and the Bismarck Archipelago is that of the endemic Fijian *P. oceanicum* A. C. Sm. (in Jour. Arnold Arb. 27: 320. 1946).

DILLENIACEAE

Hibbertia Andr. This large genus of at least 110 species (Gilg & Werdermann in E. & P. Nat. Pfl. ed. 2. 21: 21–30. 1925) occurs abundantly in Australia and New Caledonia, with two species in New Guinea (cf. A. C. Sm. in Jour. Arnold Arb. 22: 497. 1941) and one in Fiji. I believe the Fijian plant to be indistinguishable from the New Caledonian *H. lucens* Brongn. & Gris.

Dillenia L. According to the recent comprehensive monograph by Hoogland (in *Blumea* 7: 1–145. 1952), *Dillenia* (including *Wormia* Rottb.) occurs from Madagascar through southern Asia, Malaysia, and Queensland to Fiji; 55 species are recognized by him. The single Fijian species, *D. biflora* (A. Gray) Martelli, is locally very abundant, and Hoogland believes that it also occurs in the New Hebrides, where Guillaumin recognized his *D. neoebudica* as a distinct species.

SAURAUIACEAE

Saurauia Willd. This very large genus (at least 250 species according to Gilg & Werdermann in *E. & P. Nat. Pfl. ed. 2. 21*: 42–45. 1925) is widely distributed in tropical America and the Old World, where it occurs from southeastern Asia through Malaysia to northern Australia and the Solomon Islands, with one locally abundant endemic, *S. rubicunda* (A. Gray) Seem., in Fiji. I find no record of the genus in the New Hebrides, and Guillaumin (*Fl. Nouv.-Caléd.* 1948) does not list it from New Caledonia.

OCHNACEAE

Brackenridgea A. Gray. This genus, erected for a single Fijian species, *B. nitida* A. Gray, is now known to occur also in Africa and from the Malay Peninsula to New Guinea and Queensland (cf. Gilg in *E. & P. Nat. Pfl. ed. 2. 21*: 74–75. 1925). Although the Fijian endemic is quite common locally, the genus is unrecorded from the intervening archipelagos as far as New Guinea.

ELATINACEAE

Elatine L. This cosmopolitan genus is supposedly known in the Pacific region, other than New Zealand, only from the Fijian record based on two collections and believed (cf. *Jour. Arnold Arb. 26*: 101. 1945) to represent *E. gratiolooides* A. Cunn., otherwise known from Australia and New Zealand.

VIOLACEAE

Rinorea Aubl. Melchior (in *E. & P. Nat. Pfl. ed. 2. 21*: 349–352. 1925) recognizes about 260 species of *Rinorea*, but many others have been more recently described. The genus is widespread in America and Africa, and in the Indo-Malaysian region it extends from southeastern Asia to Micronesia, New Guinea, the Solomon Islands, and Fiji, where the endemic *R. storckii* (Seem.) Melchior terminates its range. *Rinorea* seems to be absent from Australia and New Caledonia.

Agatea A. Gray. *Agatea* (Melchior in *op. cit.* 360–361. 1925) has a compact range in New Guinea, the Solomon Islands (Merr. & Perry in *Jour. Arnold Arb. 24*: 209. 1943), New Caledonia, and Fiji, where its distribution ends in the endemic *A. violaris* A. Gray. There are about 13 species in the genus.

BEGONIACEAE

Begonia L. This widespread genus appears not to be indigenous in the Pacific east of Fiji, where it is represented by the endemic *B. vitiensis* A. C. Sm. The genus has been listed from the New Hebrides without mention of a species.

THYMELAEACEAE

Gonostylus Teijsm. & Binn. About 22 species are now believed to represent *Gonostylus*, which has a distribution extending from the Malay Peninsula through the Philippines and New Guinea to the Solomon Islands and Fiji, where the range is ended by the endemic *G. punctatus* A. C. Sm. A key to the species and further comments are provided by Airy Shaw (in Kew Bull. 1947: 9-16. 1947, 1950: 138-147. 1950) and C. T. White (in Jour. Arnold Arb. 31: 96. 1950).

ALANGIACEAE

Alangium Lam. The range of *Alangium* extends from southeastern Asia and Africa to Australia, Malaysia, and Melanesia, where it occurs in the Solomon Islands, New Caledonia, and Fiji. The widespread *A. villosum* (Bl.) Wang. terminates in Fiji with an endemic subspecies, subsp. *vitiense* (A. Gray) Bloemb., according to the comprehensive treatment of Bloembergen in Bull. Jard. Bot. Buitenz. III. 16: 139-235. 1939.

MYRTACEAE

Cleistocalyx Bl. In their informative revision of *Cleistocalyx*, Merrill & Perry (in Jour. Arnold Arb. 18: 322-343. 1937) indicate its range as southeastern Asia through Malaysia to northern Australia, New Caledonia, and Fiji; they do not mention any records from the Solomon Islands or the New Hebrides. The five endemic Fijian species, terminating the generic range, are separated from the rest of the genus as section *Acicalyptus* (A. Gray) Merr. & Perry.

Piliocalyx Brongn. & Gris. This supposedly endemic New Caledonian genus, with eight species (according to Guillaumin, Fl. Nouv.-Caléd. 247. 1948), has recently been reported from Fiji by Perry (in Jour. Arnold Arb. 31: 370. 1950), who identifies the Fijian material as *P. wagapensis* Brongn. & Gris, one of the New Caledonian species.

Cloëzia Brongn. & Gris. Ten species of *Cloëzia* (*Mooria* Montr.) are known, eight of them from New Caledonia (cf. Guillaumin, Fl. Nouv.-Caléd. 236. 1948), one from the Philippines (Merr. Enum. Phil. Fl. Pl. 3: 182. 1923), and one from Fiji. The correct name for this concept appears to be *Cloëzia* Brongn. & Gris (1863), because *Mooria* Montr. (in Mém. Acad. Sci. Lyon II. 10: 207. 1860) is a homonym of *Moorea* Lem. (1854, = *Cortaderia* Stapf, nom. conserv.). The different spelling used by Montrousier might conceivably be taken to indicate that these names are not homonyms, but actually *Mooria* was named after Charles Moore, Director

of the Botanic Garden in Sydney, and therefore is an orthographic variant of *Moorea*, the correct form (cf. Int. Code, Rec. 82B. 1952). Guillaumin, indeed, used the spelling *Moorea* for the myrtaceous genus (loc. cit.). In view of these facts, the endemic Fijian plant should be known as *Cloëzia microphylla* (A. C. Sm.) comb. nov. (*Moorea microphylla* A. C. Sm. in Bishop Mus. Bull. 141: 110. fig. 57, e-g. 1936).

Tristania R. Br. *Tristania*, with approximately 30 species, is distributed from southeastern Asia through Malaysia to New Guinea, Australia, and New Caledonia, and is represented in Fiji by an outlying endemic, *T. vitiensis* A. C. Sm. I find no record of the genus in the Solomon Islands or the New Hebrides.

ARALIACEAE

Plerandra A. Gray. The distribution of *Plerandra* extends westward at least to New Guinea and eastward through the Solomon Islands to Fiji; I do not find it recorded from the New Hebrides. In Fiji there are at least seven endemic species and probably more, as some seem still to be undescribed.

VACCINIACEAE

Paphia Seem. Although apparently only five binominals have thus far been referred to *Paphia*, giving the genus a distribution in New Guinea, Queensland, and Fiji, it is probable that several other Papuasian species described under *Agapetes* (cf. Sleumer in Bot. Jahrb. 70: 95-106. 1939) belong here. Sleumer's reduction of *Paphia* to *Agapetes* is not accepted by Airy Shaw (in Kew Bull. 1948: 77-104. 1948), who limits *Agapetes* to 64-67 continental species. In any case, the Fijian *Paphia vitiensis* Seem. represents the eastern limit of the generic concept.

EPACRIDACEAE

Leucopogon R. Br. *Leucopogon*, with many species in Australia and New Caledonia, reaches the eastward extension of its range in Fiji, where it is represented by *L. cymbulae* Labill. This species is fairly frequent locally, as in northern Vanua Levu; it also occurs in New Caledonia and the New Hebrides.

MYRSINACEAE

Tapeinosperma Hook. f. As revised by Mez (in Pflanzenr. 9 [IV 236]: 162-171. 1902), *Tapeinosperma* includes 26 species, but this number has been approximately doubled since then. The genus centers in New Caledonia but ranges from Australia and New Guinea through the New Hebrides to Fiji, where 11 endemic species are known.

SYMPLOCACEAE

Symplocos Jacq. The huge genus *Symplocos*, with several hundred species in America and the Indo-Malaysian region, extends eastward in the Old World to Micronesia, the New Hebrides, New Caledonia, and Fiji,

where its range is terminated by two endemic species, *S. leptophylla* (Brand) Turrill and *S. turrilliana* A. C. Sm.

LOGANIACEAE

Strychnos L. The large and widespread genus *Strychnos*, with many species in America and Africa, has been discussed in its Asiatic range by A. W. Hill (in Kew Bull. 1911: 281-302. 1911, 1917: 121-210. 1917). The Indo-Malaysian range of the genus extends to New Guinea and northern Australia, with a single outlying terminating species, *S. vitiensis* A. W. Hill, in Fiji. I have not noted references to the genus in the archipelagos between New Guinea and Fiji.

Couthovia A. Gray. Centering in New Guinea, the range of *Couthovia* extends from the Philippines and Celebes to Micronesia, New Caledonia, the New Hebrides, and Fiji, where six endemic species terminate it (cf. A. C. Sm. in Sargentia 1: 99-107. 1942).

APOCYNACEAE

Pagiantha Markgraf. As discussed by Markgraf (in Notizbl. Bot. Gart. Berlin 12: 540-552. 1935), *Pagiantha* has a distribution from continental Asia through the Philippines into Melanesia, terminating in a single endemic Fijian species, *P. koroana* Markgraf. I have already (in Jour. Arnold Arb. 33: 114. 1952) suggested that his name must fall into the synonymy of *P. thurstonii* (Baker) A. C. Sm.

Carruthersia Seem. This genus extends from the Philippines to the New Hebrides and Fiji, having two endemic species in the latter archipelago, *C. scandens* Seem. and *C. latifolia* Gillespie.

Parson sia R. Br. As taken to include *Lyonsia* R. Br., *Parson sia* extends from continental Asia through Malaysia to Australia, New Caledonia, the New Hebrides, and Fiji, where it is represented by the endemic *P. laevis* (A. Gray) Markgraf, from which *P. smithii* Markgraf, in my opinion, is scarcely distinct.

ASCLEPIADACEAE

Gymnema R. Br. This genus occurs from Africa into Malaysia, Australia, New Caledonia, and Fiji, where it is represented by two endemic and rather infrequent species, *G. stenophyllum* A. Gray and *G. subnudum* A. Gray.

VERBENACEAE

Gmelina L. *Gmelina*, with about 34 species, has a range extending from Africa and southeastern Asia through Malaysia to Micronesia, the Solomon Islands, New Caledonia, and Australia, with an outlying endemic species, *G. vitiensis* Seem., in Fiji.

ACANTHACEAE

Dyschoriste Nees. The endemic Fijian representative of this genus, *D. repanda* (A. Gray) A. C. Sm., marks the eastern limit of the Asiatic-

Malaysian portion of the genus, which also has species in America and Africa. The American species have been revised by Kobuski (in Ann. Mo. Bot. Gard. 15: 9-90. 1928).

RUBIACEAE

The Rubiaceae is not only the largest family of plants in Fiji, from the point of view of number of indigenous species, but it is also the most interesting in its distribution. Here seven genera occur on the eastern border of their ranges, while five others are believed endemic.

Xanthophytum Reinw. ex Bl. This little genus, of approximately twelve species, occurs from southeastern Asia through the larger islands to New Guinea, with one endemic outlying species in Fiji, *X. calycinum* (A. Gray) Benth. & Hook. f. ex Drake. No occurrence of the genus in the New Hebrides or Solomon Islands has been noted.

Lindenia Benth. *Lindenia* has a curious, if not incredible, distribution, being known from Central America, New Caledonia, and Fiji. A distribution of this sort must be checked by a specialist in the family before it can be taken at face value. The American population is generally treated as a single species, occurring with some frequency from Mexico to Panama. *Lindenia vitiensis* Seem., described from Fiji, is certainly infrequent there; it has also been accredited to New Caledonia, although another species has been described from that island. Seemann's note on the occurrence of *L. vitiensis* in Samoa (Fl. Vit. 430. 1873) is based on a Graeffe collection; until this record is further supported one may suspect that Graeffe's specimen was from Fiji, as his labels are not too dependable.

Dolicholobium A. Gray. Like several other genera, *Dolicholobium* was believed endemic to Fiji long after its description, until 1900 in this case. It is now known to consist of about 23 species, distributed from the Philippines (2) through New Guinea (8), the Bismarcks (1), the Solomons (6), and the New Hebrides (1) to Fiji (5). The species are all considered endemic to their respective groups. Fosberg (in Sargentia 1: 118-119. 1942) suggests that there may be only two species in Fiji, but this disposition needs to be examined.

Sukunia A. C. Sm. The single species referred to this endemic genus, *S. pentagonioides* (Seem.) A. C. Sm. (in Bishop Mus. Bull. 141: 137. 1936), is rare in Fiji. I consider the closest relationship of the plant to be with the widespread *Randia* L.

Airosperma Lauterb. & K. Schum. A single Fijian endemic, *A. trichotomum* (Gillespie) A. C. Sm., terminates the range of this small genus, which otherwise is known only from four New Guinean species. A discussion of *Airosperma* and *Abramsia* Gillespie was given by me in Jour. Arnold Arb. 26: 107-108. 1945.

Mastixiodendron Melchior. Like the preceding, *Mastixiodendron* is an essentially New Guinean genus of narrow distribution, with three species occurring from Halmahera to the Solomon Islands (cf. Merr. & Perry in

Jour. Arnold Arb. 26: 254-256. 1945) and two species endemic to Fiji (cf. A. C. Sm. in op. cit. 108-110. 1945, where the supposedly endemic genus *Dorisia* Gillespie is reduced).

Readea Gillespie. The type-species of this endemic genus, *R. membranacea* Gillespie, is fairly frequent in Fiji; two rarer plants, of which the generic position is not entirely certain, have been placed here by Fosberg (in Sargentia 1: 136-137. 1942). The general relationship of *Readea* is with *Psychotria* L.

Gillespiea A. C. Sm. Another endemic Fijian genus, monotypic as far as known, is *Gillespiea* (in Bishop Mus. Bull. 141: 158. 1936), which is also related to *Psychotria*. The single species, *G. speciosa* A. C. Sm., has been found only on Vanua Levu.

Hedstromia A. C. Sm. Like the preceding, *Hedstromia* (op. cit. 146. 1936) is a monotypic endemic, its species, *H. latifolia* A. C. Sm., being known only from Vanua Levu. *Hedstromia* is also referred to the Psychotriaceae.

Amaracarpus Bl. Approximately 60 species of *Amaracarpus* have been described, the genus occurring from the Malay Peninsula through Malaysia to Micronesia, New Guinea (42 species), the Solomon Islands (1 species), and Fiji, where the endemic *A. musciferus* A. C. Sm. terminates the range.

Squamellaria Becc. This endemic genus (Beccari, Malesia 2: 228-230. 1886) is represented by two Fijian species, *S. imberbis* (A. Gray) Becc. and *S. wilsonii* (Horne ex Baker) Becc.

Hydnophytum Jack. Approximately 100 species of *Hydnophytum* have now been described, about 60 of them from New Guinea (cf. Merr. & Perry in Jour. Arnold Arb. 26: 14-26. 1945). The genus is distributed from southeastern Asia through Malaysia to the Solomon Islands and Fiji, where five endemic species terminate its range.

CUCURBITACEAE

Neoalsomitra Hutchinson. In establishing this genus, Hutchinson (in Ann. Bot. n.s. 6: 97 seq. 1942) recognizes 22 species, ranging from India to Australia, New Guinea, and Formosa. One species, *N. integrifoliola* (Cogn.) Hutchinson, is also reported from Fiji, on the basis of a specimen collected by Horne on Vanua Levu. The species is not known to me from any other Fijian collection, and I suspect that the record may be discounted on the basis of a misidentification (Horne's specimens often being inadequate) or a mixed label. Until more recent collections indicate the contrary, the range of *Neoalsomitra* may be suspected to terminate in New Guinea.

DISCUSSION

Of the 445 phanerogam genera represented by indigenous species in Fiji (8), 101 have ranges that terminate there. Of these, 13 genera are

TABLE 1

DISTRIBUTION OF PHANEROGAM GENERA WITH RANGES TERMINATING IN FIJI

FAMILY	NO. OF GENERA	WIDE-SPREAD	INDO-MALAYSIAN	AUSTRALIA-N. CALEDONIAN	AUSTRALIA-ENDEMIC
Podocarpaceae	2	1			1
Araucariaceae	1		1		
Triuridaceae	1		1		
Palmae	8	1	2		5
Orchidaceae	7	1	6		
Balanopsidaceae	1			1	
Proteaceae	1			1	
Santalaceae	1		1		
Amaranthaceae	1		1		
Ranunculaceae	1	1			
Menispermaceae	1		1		
Degeneriaceae	1				1
Annonaceae	5	3	2		
Cunoniaceae	2		1	1	
Connaraceae	1	1			
Leguminosae	4	2	1	1	
Linaceae	1		1		
Rutaceae	1		1		
Simaroubaceae	1				1
Malpighiaceae	1		1		
Euphorbiaceae	6	4	1	1	
Anacardiaceae	1			1	
Celastraceae	1	1			
Hippocrateaceae	1	1			
Sapindaceae	2	1	1		
Rhamnaceae	2	1	1		
Vitaceae	2	1	1		
Tiliaceae	2	1	1		
Sterculiaceae	3	1	1		1
Dilleniaceae	2	1			1
Saurauiaceae	1	1			
Ochnaceae	1	1			
Elatinaceae	1	1			
Violaceae	2	1		1	
Begoniaceae	1	1			
Thymelaeaceae	1			1	
Alangiaceae	1	1			
Myrtaceae	4		2	2	
Araliaceae	1		1		
Vacciniaceae	1			1	
Epacridaceae	1				1
Myrsinaceae	1				1
Symplocaceae	1	1			
Loganiaceae	2	1	1		
Apocynaceae	3			3	
Asclepiadaceae	1	1			
Verbenaceae	1	1			
Acanthaceae	1	1			
Rubiaceae	12	1	6		5
49 Families	101	34	43	11	13

endemic and perhaps not significant in this discussion (although their relationships are without exception toward the west). The remaining 88 genera fall into three general patterns of distribution: 34 of them are widespread, with some species in Africa and/or America as well as in Indo-Malaysian regions; 43 are Indo-Malaysian, although a few extend northwestward as far as China and Japan, while some are limited to the Melanesian archipelagos; and eleven have a predominantly "Australian—New Caledonian" type of distribution. It seems desirable to treat the widespread genera as "terminating" in Fiji, since even when they occur in South America there is no evidence that trans-Pacific migration was involved in the modern distribution; on the other hand, the relationships of the constituent species of these genera indicate that they reached Fiji by an eastward extension of the Indo-Malaysian portion of their ranges. Apparent contradictions of this statement are found in such genera as *Stillingia* (Euphorbiaceae) and *Lindenia* (Rubiaceae), discussed above; but in these cases the disjunction of their ranges is so extraordinary that the need of re-examination of generic lines is indicated.

It is seen, then, that nearly 23 percent of the phanerogam genera with indigenous species in Fiji extend no farther eastward. This figure is perhaps more impressive when one considers that the remaining genera (344 in number) include many common strand plants or plants with wind-carried seeds, to which the over-water distance to Polynesian archipelagos is not a serious obstacle. Most of the genera terminating in Fiji are groups of forest plants, often with heavy seeds, and it may be suspected that land connections were needed to permit their forbears to reach this region. For the most part the Fijian species of these genera are endemic, indicating that the isolation of the archipelago from other remnants of the foundered Melanesian continent has been of considerable duration.

To carry this study to a logical conclusion, similar statistics should be obtained from each archipelago between New Guinea and the American continent. Although this has been done for some island groups in a preliminary way (3), we still lack information to show where in the Pacific the important distributional discontinuities in the ranges of Indo-Malaysian genera occur, and to show also where new elements with relationships to the east become significant. Obviously such data are not obtainable in advance of fairly complete floristic studies, but upon them depends a better comprehension of Pacific phytogeography. It is hoped that this summary will contribute to the final picture; it indicates, I believe, that a sharp distributional break in the continuity of phanerogam genera occurs in or immediately east of Fiji, and it strengthens the premise that this line marks a geological boundary of fundamental significance.

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MITOCHONDRIA AND PRECIPITATES OF A-TYPE VACUOLES IN PLANT CELLS

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With three plates

THE ULTIMATE PURPOSE of investigations of cytoplasmic particulates is to determine their function, and this requires the study of living material. The development by Bailey (1) of special techniques for examining living cambial cells, and the study of different properties of vacuoles in relation to staining with vital dyes by Bailey and Zirkle (2) demonstrated the general importance and practicability of living studies in the investigation of protoplasts. The introduction of phase contrast microscopy added another valuable method to such study; and, in combination with vital staining and use of polarized light, made possible the observation and in many cases identification of cytoplasmic components in different types of living cells.

The distinction between mitochondria, plastids, and spherosomes in the epidermal cells of a number of plants has been considered in previous studies [Sorokin (18, 19, 20)]. Present investigations are primarily concerned with the identification of mitochondria and their distinction from precipitates of A-type vacuoles.

Two types of vacuoles are encountered in the living cells of higher plants (Bailey, 1; Bailey and Zirkle, 2; Zirkle, 23). One, the A-type vacuole, becomes intensely magenta or red in aqueous solutions of either Neutral red or Methyl red, while the other, or B-type vacuole, stains orange or reddish-orange in aqueous solutions of Neutral red, but gives no color with Methyl red. A-type vacuoles contain aromatic substances, and tend to form copious dark precipitates with dyes of the type of Neutral red or Janus green B. Because the recognition of mitochondria in living plant cells is based upon their reversible staining with Janus green B, it is important to differentiate them from precipitates of A-type vacuoles when the latter are formed in the cells. It is no less important to distinguish them from the spherosomes (oil globules), which may reflect a delicate green color after the cell preparation has undergone prolonged staining. Hence, the criteria for the recognition of mitochondria are further elaborated here, and to these are added a method for the discrimination of mitochondria and the A-type vacuolar precipitates, using combined vital staining with Janus green B and Neutral red.

Although the ubiquity of mitochondria in living cells is usually taken for granted, there has been no definite demonstration of their permanent

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presence in many plant tissues, including the chloroplast-containing cells of the leaf (Weier, 21; Weier and Stocking, 22). The present study is therefore also concerned with demonstration of ubiquitous occurrence of mitochondria in various chloroplast-containing cells of leaf tissues.

MATERIAL AND METHODS

Because the epidermal and subepidermal cells of lettuce exhibit characteristic A-type vacuoles, while spinach cells show the presence of B-type vacuoles, these plants were selected for this study. Living cells showing cyclosis, or otherwise characterized as being alive by Bailey and Zirkle (2), were considered, only. In the midrib of commercially grown Iceberg lettuce small incisions were made by razor blade. The pieces of epidermis were then stripped off by forceps and floated upon either 10 per cent sucrose (Merck reagent) solution, or 10 per cent commercial sucrose solution. Both double-distilled water and tap water were used. The pH values of the solutions were determined by Beckman's glass electrode pH meter. Similar procedures were followed with strips of epidermis from the petioles of commercially grown spinach. Cross sections from lettuce midribs and spinach petioles were also taken. To insure aerobic conditions during the experiment these sections were made adherent to a piece of wood splinter, which was extended across the flat staining dish, and so were also floated upon the solutions. All solutions were freshly prepared at the beginning of each experiment, and upon addition of sucrose the water was vigorously agitated to incorporate air. Observations were made either immediately after securing the preparations under the phase contrast microscope, or after staining with Janus green B (Hoechst), Neutral red (NACC, NX-6), or a combination of the two dyes. The former was added to the sucrose solutions in dilutions of 1:50,000, while the latter was added to make a dilution of 1:20,000. When used in combination the final solutions of the dyes were mixed together in equal amounts. An average of 45 minutes was allowed for the penetration of the dye, and, with few exceptions, material was examined and photographed during the following hour.

Observations were made under the Zeiss Opton microscope with bright field, phase contrast, and polarization equipment. Neofluar objectives 40/0.75; Ph 40/0.75, Ph 100/1.30, Apochr. 90/1.4 were used with K oculars 8X with magnification changer for factors 1X, 1.6X, and 2.5X. Photomicrographs were made with a 35 mm. camera attachment (R. Winkel G. m. b. H.) Negatives were enlarged as specified.

OBSERVATIONS

The epidermal tissue of lettuce peels off in two layers, the epidermal proper, and the subepidermal. The epidermal cells of the midrib, seen in surface view, have pointed ends, while transverse walls of subepidermal cells are oblique (Hayward, 9). The first material is observed to better

advantage if mounted on the slide with the cutinized side uppermost. Subepidermal cells are better seen when the material is mounted in the reverse way. Both produce an excellent phase contrast when in living condition. In most of the epidermal cells the nucleus is located centrally and is surrounded by a circle of round formed plastids, which are predominantly arranged in a plane parallel to the surface of the cell (PL. I, FIG. 2, FIG. 4). However, individual plastids may occur in small numbers at different planes (PL. I, FIG. 1). Although the lettuce tissue is almost etiolated, the round plastids may show a slight green coloring. There is a constant motion of cytoplasm in the vicinity of the nucleus, and the streams circulate the particles through trabeculae towards the peripheral layers of cytoplasm. The most conspicuous particles, easily recognizable under phase contrast, are the spherosomes (PL. I, FIGS. 1 and 4). The spherosomes move faster than any other component of the cytoplasm, are highly refractive, and when observed under oil immersion appear as plates with rounded corners which revolve about their axis and continually change the phase contrast from dark to light. Similar behavior was observed in spherosomes of other plant cells (Sorokin, 20). Besides the spherosomes there are other components which can be observed under phase contrast, but cannot be identified without application of vital staining. These are the mitochondria and colorless plastids. The existence of polymorphic colorless plastids in the epidermal, subepidermal, and parenchyma cells of lettuce can be established by exposing head lettuce material to sunlight for 10 or more days in a moist chamber. After this period the exposed material becomes quite green; and numerous polymorphic green plastids of various sizes, including small granules, dumb-bells, and threadlike forms, can be observed in the cells. The existence of mitochondria in the epidermal and subepidermal cells can be tested by the reaction of such particulates to vital staining with Janus green B. In PL. I, FIG. 2 mitochondria are stained blue and appear in the layer of cytoplasm furthest from the cutinized cell wall. This material was mounted cutinized wall down and was photographed through the subepidermal cell, the outlines of which are visible in the photograph. Similarly, blue stained mitochondria may be seen in the photograph of a subepidermal cell (PL. I, FIG. 3). In both cases mitochondria are quite similar in shape and in about equal number. Besides the spherosomes the other particulate which does not stain with Janus green B after about 45 minutes is the colorless polymorphic plastids. They appear in varying numbers in different cells, and are prominent in the vicinity of the nucleus (PL. I, FIG. 1) and in the parietal layers of the cytoplasm, including that layer next to the cutinized cell wall from which the majority of mitochondria are excluded. That the polymorphic colorless plastids of lettuce may have sizes and shapes very similar to those of mitochondria was observed before (Sorokin, 19). Present photographs lack color distinction, but in PL. I, FIG. 5 it is still possible to see darker forms, mitochondria stained with Janus green B, and lighter forms, unstained plastids.

In cells stained with Janus green B a precipitate begins to form in the

vacuole after a varying period of time, from 1-2 hours. Discrete small granules at first begin to join others to form larger bodies, and at certain stages the staining reaction is so confusing that only an experienced observer can pick out the mitochondria in the preparation. In PL. II, FIGS. 6 and 7 the same cell is pictured at different foci. There vacuolar precipitates are beginning to form in several portions of the vacuole; and although the mitochondria are still colored, they are not clearly distinguished. However, staining with combined Janus green B and Neutral red will precipitate the heavy colloidal substance as a dark cherry-red deposit, while the mitochondria will remain blue. With the passage of time the precipitate increases in amount, to become copious. In PL. II, FIG. 8 the precipitate was dark red, while blue mitochondria could also be discerned. The chloroplasts retained their position in a circle about the nucleus. In PL. II, FIG. 9 a similar precipitate was found in guard cells and adjacent cells. Chloroplasts, mitochondria, and spherosomes were also observed in guard cells. In subepidermal cells the precipitate was finer in structure, copious, and more of an orange-red tint. Janus green B alone will produce in subepidermal cells a precipitate, similar in grain, but of brilliant blue color which refracts green (PL. II, FIG. 10). In epidermal cells Janus green B alone will not produce the heavy clumps typical for those with Neutral red or combination staining. Instead, isolated blue granules and smaller clumps become visible there. Thus, cross sections of the leaf midrib stained with the combined stains reveal precipitates of A-type vacuoles in both epidermal and subepidermal cells.

The cells of parenchyma tissue may show a diffuse reddish coloring with Neutral red or combination staining; but, with very few exceptions, fail to show typical precipitates. The latter occurs, however, in the cells of the bundle sheaths enclosing the vascular bundles.

The character of the precipitate in cells of the bundle sheaths is reminiscent of that found in subepidermal cells in that it is finer grained and lighter red than that of epidermal cells.

Material treated for 24 hours with ferrous chloride solution, one of the tests for tannins, showed a blue-black deposit in epidermal cells, but none in subepidermal or bundle sheath cells. It would seem that substances precipitated by the stains in these differing cells are not the same.

The presence of mitochondria, spherosomes, and plastids were observed in all cells in the cross sections of lettuce midrib studied.

Experiments with spinach were carried out simultaneously with those on lettuce. Pieces of tissue peeled from the petioles of leaves contain epidermal cells with attached subepidermal tissue. In spinach the layer of subepidermal cells found in lettuce is lacking; and the collenchyma tissue does not form a complete cylinder of even thickness immediately under the epidermis, but is more developed in some parts of the petiole, compared with other parts of the same petiole, so as to form little ridges. This condition is similar to that found in the petiole of the beet (Hayward, 9). Therefore, peelings of epidermis may have attached either collenchyma cells or the chlorophyll-bearing parenchyma. Chloroplasts of the latter

may completely fill the cells, or may occur in fewer numbers, to render them suitable for living observations.

The phase contrast optics do not produce such excellent images in spinach as they do in lettuce, but are helpful in the identification of some of their components. PLATE III, FIGS. 11 and 12 show the same epidermal cell stained with a combination of Janus green B and Neutral red and photographed with light and phase contrast objectives of the same magnification. In both cases the chloroplasts and the mitochondria are clearly identifiable. In PL. III, FIG. 11 mitochondria were stained medium blue, the chloroplasts green, and the vacuolar precipitate a bright red. Under phase contrast, PL. III, FIG. 12, the mitochondrial color was lost, and they appeared as black spherical bodies. The chloroplasts showed more structural details, but the vacuolar precipitate had lost some of the sharpness of outline seen in the light microscope. The spherosomes are difficult to photograph in spinach, due to their small size and rapid motion. They are best observed in cells with pronounced cytoplasmic streaming and in the trabeculae which cross the vacuoles. In PL. III, FIG. 13 a large chlorophyll-bearing parenchyma cell stained with Janus green B was photographed under the light microscope. The preparation had been mounted cuticle side down. The distribution of chloroplasts and the stained mitochondria was uniform throughout the cell. PL. III, FIG. 14 is a photograph of a section of a similar cell at high magnification. Again, the mitochondria were distinct and colored and opaque medium blue at the moment recorded.

In cross sections of the petiole the chlorophyll-bearing parenchyma may occupy from one to several layers, gradually merging with the large cells of the ground parenchyma of the petiole. These large cells show a remarkable development of cytoplasmic trabeculae, which not only cross the vacuole, but form a complex three-dimensional net in which the nucleus is suspended. The chloroplasts are much smaller there than in the chlorophyll-bearing parenchyma; and, together with mitochondria and spherosomes, move about in the cytoplasmic strands. Such a cell, stained with combined Janus green B and Neutral red, showed blue colored mitochondria after one hour and thirty minutes' observation under the microscope. Later the mitochondria lost their color, but the cell remained alive and was observed under the microscope for eight hours. During these observations the trabeculae changed their lengths; and the bulk of the cytoplasm with the suspended nucleus altered its position, gradually moving from one side of the cell to the other.

Staining with the combination of Janus green B and Neutral red gave no A-type vacuolar precipitates in the epidermal and chlorophyll-bearing parenchyma cells of spinach. The guard cells showed magenta colored vacuoles, but unlike those in lettuce did not form precipitates. Precipitates of any colored type were conspicuously absent from the cells of the bundle sheath; yet, they contained chloroplasts, mitochondria, and spherosomes. However, epidermal cells, particularly those in the neighborhood of the stomata, evinced globular red-colored precipitates, such as are shown in PL. III, FIG. 11. This type of precipitate, formed close to the surface of

the vacuole, is characteristic of B-type vacuoles (Bailey and Zirkle, 2; Zirkle, 23).

During staining experiments it was noticed that the color of the combination stain in sucrose solution differed with use of tap or double-distilled water, being brown-violet in the former and amethyst in the latter. To determine the pH values of solutions used and their effects upon staining of mitochondria and upon formation of precipitates in the vacuoles, tests were made and are summarized in TABLE I.

The brand NX-6 of Neutral red in tap water (pH 7.2) and dilution 1:20,000 was red-orange (pH 6.7). In double-distilled water (pH 6.0),

TABLE I

Source of water & dyes pH	Color	Lettuce			Spinach		
		Mit.	A-type	B-type	Mit.	A-type	B-type
Win.tap *	7.2						
Win.tap JgB	6.9	Blue	X	X	...	XXX	...
Win.tap Nr	6.7	Red-orange	..	XXX	X
Win.tap JgB Nr	6.85	Brown-violet	X	XXX	..	XXX	..
Win.tap 10% com. suc.	7.1						
Win.tap 10% com. suc.							
JgB	7.0	Blue	X	XXX	..	XXX	..
Win.tap 10% com. suc.							
Nr	6.65	Red-orange	..	XXX	X
Win.tap 10% com. suc.							
JgBNr	6.8	Brown-violet	X	XXX	..	XXX	..
Win.tap 10% re. suc.	6.7						
Win.tap 10% re. suc.							
JgB	6.7	Blue	X	XXX	..	XXX	..
Win.tap 10% re. suc.							
Nr	6.5	Red-orange	..	XXX	X
Win.tap 10% re. suc.							
JgBNr	6.6	Brown-violet	X	XXX	..	XXX	..
D.dis.	6.0						
D.dis.JgB	5.25	Blue	X	X	..	XXX	..
D.dis.Nr	5.05	Cherry-red	..	XXX
D.dis.JgB Nr	5.175	Amethyst	X	XX	..	XXX	..
D.dis. 10% com. suc.	5.8						
D.dis. 10% com. suc.							
JgB	5.7	Blue	XXX	XXX	..	XXX	..
D.dis. 10% com. suc.							
Nr	5.4	Cherry-red	..	XXX
D.dis. 10% com. suc.							
JgBNr	5.5	Amethyst	XXX	XXX	..	XXX	..
D.dis. 10% re. suc.	5.7						
D.dis. 10% re. suc. JgB	5.65	Blue	XX	XX	..	XXX	..
D.dis. 10% re. suc. Nr	5.15	Cherry-red	..	XXX	X
D.dis. 10% re. suc.							
JgBNr	5.3	Amethyst	XX	XXX	..	XXX	..

* The abbreviations stand for following: Win. = Winchester; JgB = Janus green B; Nr = Neutral red; com. suc. = commercial sucrose; re. suc. = reagent sucrose; D.dis. = double distilled; Mit. = mitochondria; XXX = excellent; XX = good; X = average staining.

similar dilution, the color was cherry-red (pH 5.05). Addition of 10 per cent sucrose tended to lower the pH values in all solutions investigated. Reagent grade sucrose lowered the values more than did commercial sugar. There was no appreciable difference in the color of solutions after addition of sucrose. The color of Janus green B remained blue regardless of the pH value of the solutions. Indeed, this was indicated for a wider range (pH 3 to pH 9) by Drawert (8). The addition of Janus green B to the solutions lowered the pH value, though to a lesser degree than the addition of Neutral red. With combination of the dyes, dilutions of 1:50,000 of the green and 1:20,000 of the red being represented in the final mixture, the solutions ranged in color from violet-brown in the higher pH ranges to amethyst in the more acidic pH values. Similarly, the pH readings of the mixed dye solutions represented mean values of the readings of the separate dye-sucrose solutions.

In determining the color of vacuoles after staining with Neutral red or the combination of dyes mentioned previously, it is essential to keep in mind that variations in intensity can be attributed to varying concentrations of the dyes in different vacuoles, to "salt" and "protein" error, etc. (Bailey, 1). In the present study, however, attention was less directed to diffuse coloring of vacuoles than to the formation of colored precipitates. Accordingly, the indications of intensity noted in the columns, "A-type" and "B-type," of TABLE I refer to the precipitate rather than to the vacuole.

The A-type precipitate in lettuce material was very good in virtually all solutions used. Globular precipitates characteristic of B-type vacuoles were observed in spinach after staining with Neutral red or with the combination stain. They were not seen when Janus green B was used alone.

The staining of lettuce mitochondria was only moderately successful in tap water with either type of sucrose used. Better results were obtained when solutions were made up in double-distilled water. Beautifully colored mitochondria were observed in all spinach cells investigated, regardless of the source of water, or of the type of sucrose used.

DISCUSSION

Cell granules and filaments which we now call mitochondria were first stained in the animal cell by Michaelis (15) in 1900. He indicated that the diethyl derivative of Janus green B was essential for the staining reaction, and that the reaction was aerobic. He advised that the procedure be carried out in flat shallow dishes. Other investigators could not repeat the reaction until Bensley (3) reintroduced its use. The history of the use of Janus green B for staining of plant mitochondria began a few years later, but has been running a parallel course. Although mitochondria in higher plants were successfully stained by N. Cowdry (6) and many subsequent observers of the living cell (for literature see Sorokin, 18, 19; Newcomer, 16), the validity and even possibility of the staining procedure is still doubted by some investigators (Newcomer, 16).

According to E. V. Cowdry (5) Janus green B (Hoechst) stains mitochondria specifically; Janus green (Grübler) and Janus green C will not stain them, though these dyes differ only in the substitution of 2 H-atoms for the first, and 2 CH₃-groups for the second, in place of the two C₂H₅-groups. A number of other Janus green B dyes, including Janus green B (Grübler, Berlin West) and Diazogreen Merck were found to stain mitochondria in plants, whereas Janus Green (Grübler, Leipzig) did not (Drawert, 8). Janus green B (diethylsafranine azodimethylaniline chloride) is blue. Upon chemical reduction Janus green B is reduced successively to leuco-Janus green B, to diethylsafranine (red), and to leucosafarine (colorless). Presumably there are several types of leuco-Janus green B (partially reduced forms), and some of them are colorless (Lazarow and Cooperstein, 11). Leuco-Janus green B can be reoxidized to the blue dye by molecular oxygen, or it can be further reduced to the diethylsafranine derivative (red dye) by splitting the azo bond. The second reduction step is not reversible (Lazarow and Cooperstein, 12).

When a mitochondrion is stained blue under aerobic conditions, the Janus green B is in an oxidized state. With the change to anaerobic environmental conditions the dye is reduced to what is presumed to be a colorless leuco-form. The latter may become oxidized again with the return to higher oxygen tensions, restoring the color to the mitochondrion under scrutiny. This property of taking up the colored stain, losing the color, and regaining it again is considered to be a specific reaction for mitochondria. Therefore, in the preceding observations, it is emphasized, only those particulates answering these conditions are here considered to be mitochondria.

The Janus green B reaction in mitochondria is strictly aerobic. This has been continuously reiterated by Bensley (3, 4). In plant cells the reaction was observed only when the pieces of material were floated upon the solution with the dye (Sorokin, 18). To assure the penetration of oxygen in staining the mitochondria from the epidermal cells of onion, Drawert (8) used pure oxygen, which was either supplied beforehand to the solution of the dye on which the strips of epidermis were floating, or was bubbled through it during the staining. In order to stain mitochondria the present author finds it sufficient to aerate the solution by means of a vigorous shaking beforehand.

The rate of penetration of the dye into the cells varies from plant to plant and from cell to cell within the same tissue. As an example, hair cells of *Tradescantia* exhibit cyclosis for hours after mounting the preparation in water with Janus green B; but mitochondrial staining becomes visible only after mechanical pressure is applied to the cover glass. The length of time during which it is possible to observe the colored mitochondria also varies before their decolorization. Drawert (8) reports that he was unable to use a coverglass and had to resort to the use of a water-immersion lens in order to see the mitochondrial reaction.

Michaelis (15) had early pointed out that vital staining does not occur when the respiration rate is very low. The present author (19) could not

obtain the mitochondrial reaction in epidermis explants from iris cultured upon an isotonic sucrose solution for 11 days. The cells were alive, but apparently the rate of respiration was low. In addition, dead cells do not reduce Janus green B, hence, no differential staining takes place (Lazarow and Cooperstein, 11). The preceding points illustrate some reasons why some investigators failed to obtain the mitochondrial reaction in plant cells. Selective staining is specific within a range of precise conditions enumerated above.

Staining of structures other than mitochondria by Janus green B may occur in cells. In dead or dying cells, showing Brownian movement, the cell wall, the cytoplasm, and the nucleus will take up the stain. Besides the colored precipitate of the A-type vacuole already discussed, the spherosomes may also acquire a refractive greenish tint. Drawert (8) has found that the spherosomes of the living onion cell begin to fluoresce green-white or green-yellow under anaerobic conditions after mitochondria stained with Janus green B lose their color. He explained this by postulating the formation of a fluorescent reduced form of Janus green B, which is adsorbed on the spherosomes.

Staining of material containing A-type vacuoles with the combined stains Janus green B and Neutral red distinguishes the vacuolar precipitates from mitochondria by color. This identification of granules occurred in all cases investigated, regardless of the pH value and color of the combined dye solutions. This combination of stains was used by Michaelis (15) for differentiation of cytoplasmic granules. In modern times it is used extensively in haematology for the identification and distinction from mitochondria of other granules in various blood cells (Romeis, 17). The present application of the method to plant material is modified, in that dilute solutions of the dyes are used to assure survival of the cells and aerobic conditions of staining.

The ubiquity of animal cell mitochondria is generally accepted, and it has been demonstrated that the cyclophorase system of enzymes is associated with them (reviewed in De Robertis et al., 7). It is also almost universally agreed that the fundamental properties of animal and plant mitochondria are analogous. Hence, it is logical to assume that the particulate responsible for the respiratory functions must be present in all living cells of plants. The presence of mitochondria in all living epidermal cells studied has been observed by the present author partly in papers cited above, partly in vast unpublished material. It is intended eventually to demonstrate the presence of mitochondria in the cells of different tissues, for which a substantial amount of material is already accumulated. In the present study mitochondria are shown in chlorophyll-bearing parenchyma, in collenchyma, and in living cells of the vascular bundle of the spinach leaf petiole, as well as in ground parenchyma and all living cells of the vascular bundles of the midrib of lettuce.

From the accounts of existing literature concerning the mitochondria of mesophyll cells, Weier (21) draws the conclusion that mitochondria are highly variable intracellular components. The identification of mitochon-

dria in the literature mentioned is based either upon the study of fixed preparations (Löwschin, 14; von Loui, 13) or upon observations of living material without vital staining (Heitz, 10). Both methods do not permit one to differentiate the cytoplasmic particulates. Mitochondrial methods in plant cells will fix mitochondria, plastids, and spherosomes, while photomicrographs of living unstained cells under the light microscope, using a low voltage lamp and blue filter, will only occasionally produce enough contrast to record the mitochondria. Significantly, however, Heitz (10) mentions the permanent presence in cells of globular structures, presumably spherosomes, of similar size to mitochondria, but distinctly different in appearance and motion.

SUMMARY

More study of cytoplasmic particulates must be made in living material, for this method offers the best hope of understanding their normal metabolic functions. Phase contrast microscopy provides a very valuable aid to the study of the living cell; and, in combination with vital staining, it is possible to observe and often to identify various components of the cytoplasm.

Observations of mitochondria in plant cells by the use of vital Janus green B staining can be confused by the presence in the cells of other granules which may acquire a blue coloring. These granules are either precipitates of A-type vacuoles or spherosomes.

Mitochondria are identified and photographed in epidermal cells, in chlorophyll-bearing parenchyma cells, in collenchyma cells, in the cells of ground parenchyma, and in the living cells of vascular bundles in both lettuce and spinach.

Spherosomes are distinctly identified in the cells of lettuce by phase contrast microscopy, so that confusion with the other particulate is impossible.

Epidermal cells of lettuce were used to study the precipitates of A-type vacuoles, and it was found that by introducing combined staining with Janus green B and Neutral red confusion of the precipitate with mitochondria could be avoided, the mitochondria staining blue, and the precipitate staining red.

No precipitate of the A-type found in some cells of lettuce were found in spinach. Instead, the cells of the petiole exhibited globular precipitates characteristic of B-type vacuoles.

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EXPLANATION OF PLATES

PLATE I. All photomicrographs were made with phase contrast optics and green filter from living cells of lettuce stained with Janus green B.

FIG. 1. Epidermal cell mounted cutin side up, showing nucleus and distribution of the following cytoplasmic particulates: large oval light green plastids; rod-shaped plastids; very small spherosomes; a few spherical mitochondria. With the exception of the latter, none of the forms was stained with Janus green B. $\times 956$.

FIG. 2. Epidermal cell mounted cutin side down, showing nucleus surrounded by oval green plastids and numerous blue colored mitochondria. Outline of a portion of subepidermal cell is visible in upper part of photograph. $\times 1069$.

FIG. 3. Subepidermal cell, showing oblique transverse walls, nucleus, few green plastids and large number of blue colored mitochondria. $\times 1190$.

FIG. 4. A portion of epidermal cell showing nucleus with a ring of green plastids and numerous spherosomes not stained by Janus green B. $\times 1105$.

FIG. 5. A portion of epidermal cell, exhibiting morphologically similar particulate. Part of the structures were stained with Janus green B (mitochondria) and part were not (colorless plastids). $\times 1105$.

PLATE II. Photomicrographs were made from living cells of lettuce stained either with Janus green B, or the combination of Janus green B with Neutral red. Except fig. 6-7, bright light optics and green filter were employed.

FIG. 6. Epidermal cell stained with Janus green B under phase contrast. Precipitate of A-type vacuole begins to form in different parts of central vacuole (irregular clumps). Nucleus, round plastids and spherosomes are distinct. Mitochondria difficult to recognize. $\times 731$.

FIG. 7. Same cell as in fig. 6, at different focus.

FIG. 8. Epidermal cell stained with combination of Janus green B and Neutral red. Copious, coarse grained, red-colored precipitate and blue colored mitochondria were observed. Nucleus was with a ring of oval plastids. $\times 979$.

FIG. 9. Guard cells. Precipitate dark red, mitochondria blue, plastids green. $\times 979$.

FIG. 10. Subepidermal cell stained with Janus green B. Precipitate brilliant blue with green refraction, finer grained and copious. $\times 979$.

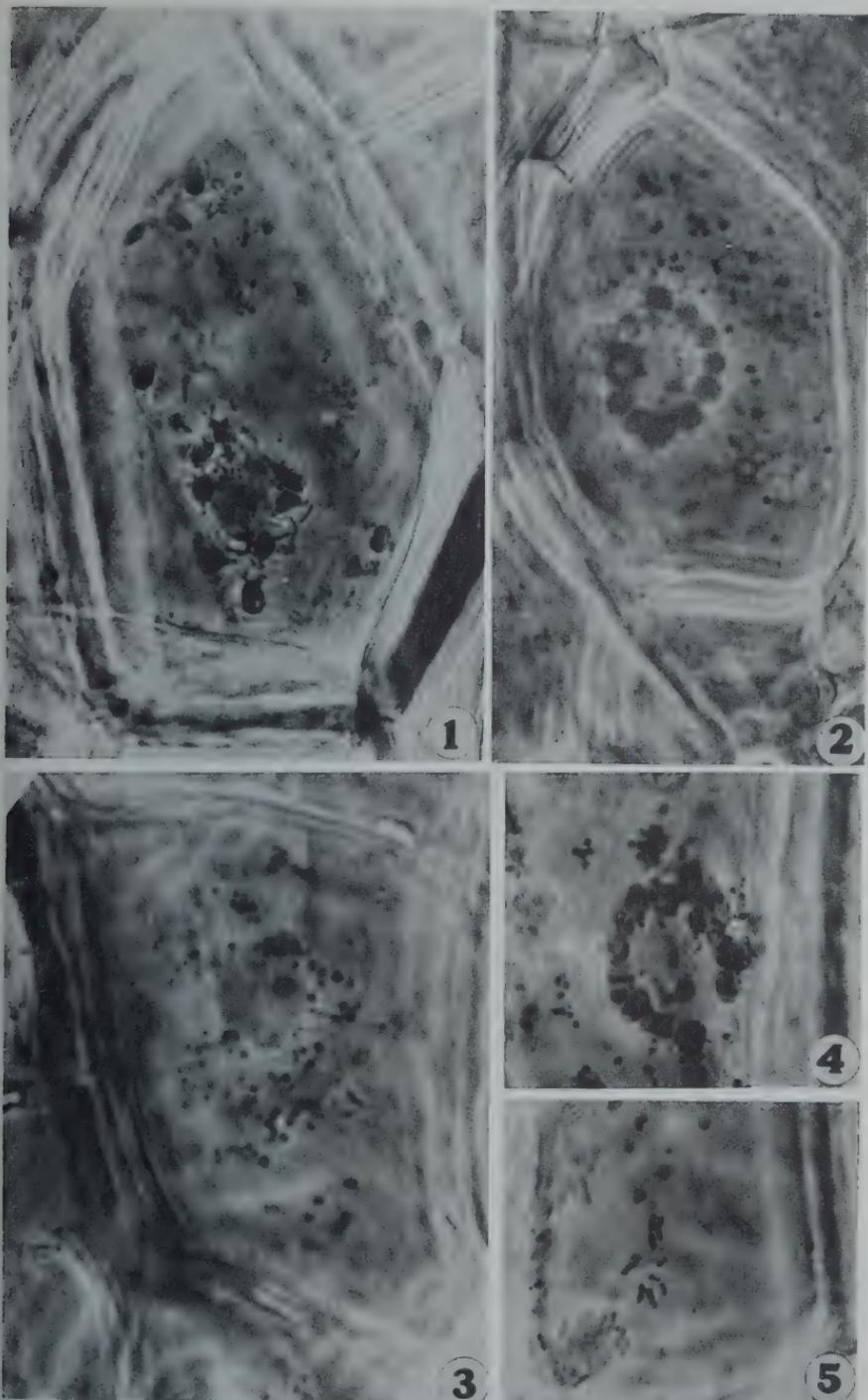
PLATE III. All photomicrographs were taken from living cells of spinach stained either with Janus green B, or the combination of Janus green B with Neutral red. With the exception of FIG. 12, all were taken under bright light optics with green filter.

FIG. 11. Epidermal cell stained with combination of Janus green B and Neutral red, showing green plastids, blue colored mitochondria, and large red colored globular precipitate typical for B-type vacuoles. $\times 1012$.

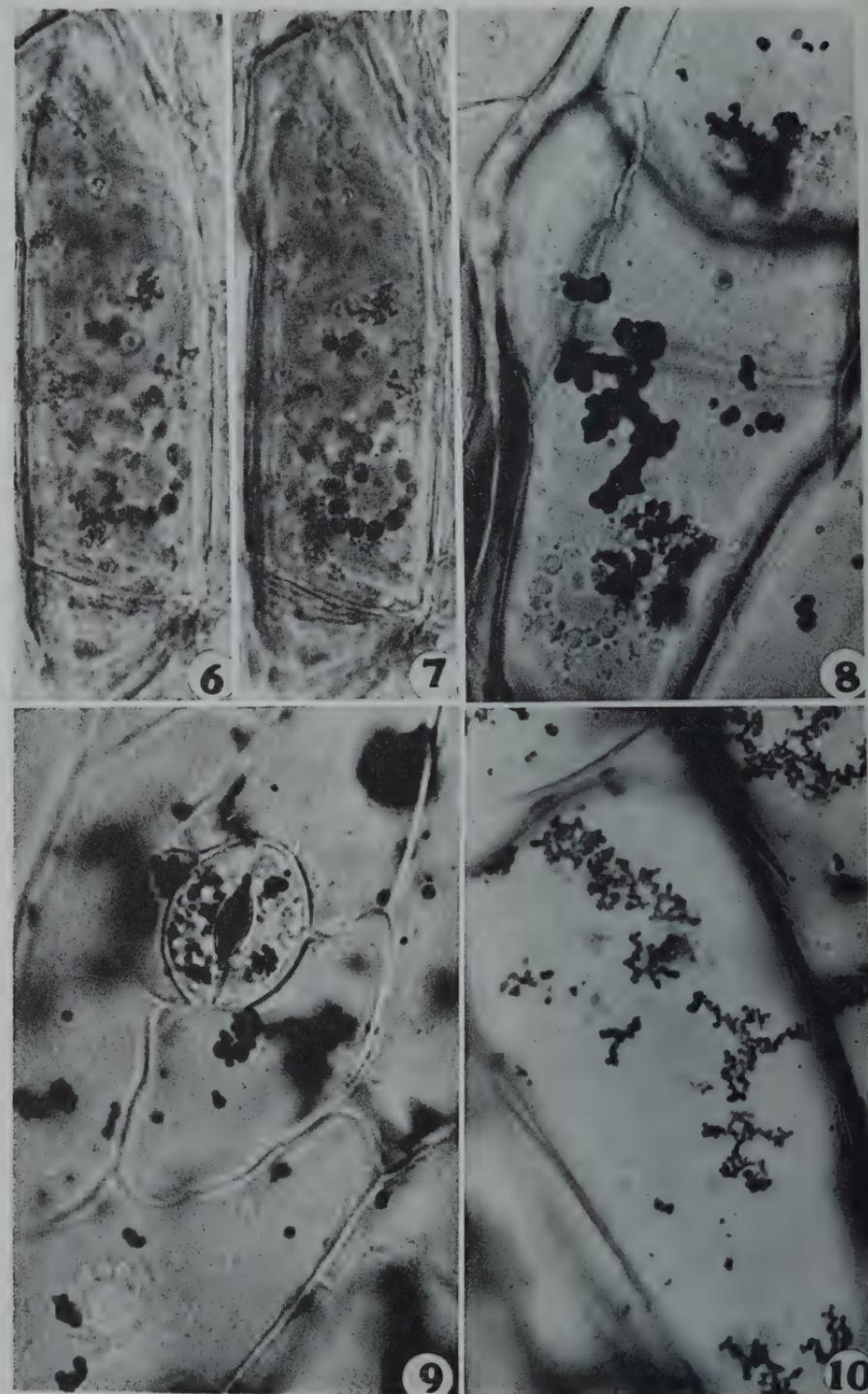
FIG. 12. Same cell as in FIG. 11 photographed under phase contrast optics. The cell shows more depth, but the sharpness of the outline of the precipitate is lost. $\times 1012$.

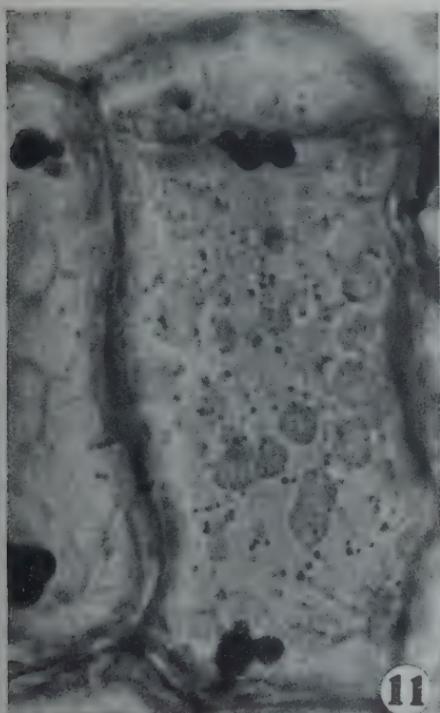
FIG. 13. A large chlorophyll-bearing parenchyma cell stained with Janus green B shows the distribution of green chloroplasts and blue colored mitochondria. $\times 698$.

FIG. 14. A portion of chloroplast-containing parenchyma cell under larger magnification, showing chloroplasts and mitochondria. $\times 1513$.

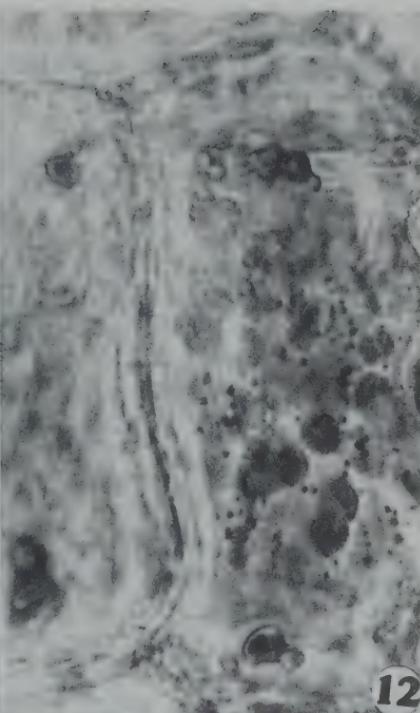


H. SOROKIN, MITOCHONDRIA AND PRECIPITATES





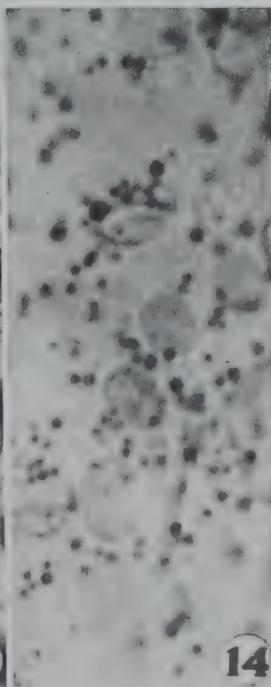
11



12



13



14

ON THE DIFFERENTIATION OF XYLEM

RALPH H. WETMORE AND SERGEI SOROKIN

With six plates

INTRODUCTION

THE TRACHEOPHYTA comprise those plants which have vascular tissues. Since xylem and phloem are almost universally associated in the histological composition of vascular tissues, it is probable that their differentiation is activated by substances present in or available to the procambial or cambial regions at essentially the same time. Descriptions now exist of the initiation of primary phloem and xylem in leaf and bud primordia and in adjacent stem tissues for enough angiosperms to suggest that the limiting factors may be different for these two tissues (Jacobs, 1952, 1954). Yet little is known of the identity of these factors in any plant. Evidence (Jacobs, 1952, 1954) supports the belief that an auxin may be of hormonal influence in removing the limitation on xylem differentiation. So far as the authors are aware, nothing is known that establishes the nature of the limiting factors in the differentiation of phloem. Nor has evidence been provided which would designate reasons for the characteristic development of primary xylem and phloem from the procambium rather than from some other tissue. That the severing of mature vascular tissues by deliberate incisions (Jost, 1940, 1942; Sinnott and Bloch, 1944; Jacobs, 1947b, 1952, 1954) can be followed by restored vascular connections across regions where no procambium existed is of arresting importance. Jacobs has recently extended his quantitative studies to show that xylem regeneration following experimental incisions is proportional to the polarized flow of auxin when the latter is in physiological concentrations.

The present investigations are the early results of a study of xylem regeneration in homogenous, parenchymatous callus (a) into which have been grafted the apical portions of shoots of the same species, or (b) instead of the grafted apices, agar containing auxin in varying physiological concentrations takes the place of the scion. Qualitative findings are reported at this time; the work must be extended to give further meaning to these studies.

MATERIAL AND METHODS

The present study has been largely conducted on *in vitro* grown explants of callus of *Syringa vulgaris* L. Preliminary studies of corresponding nature have been made on *Parthenocissus tricuspidata* (Sieb. & Zucc.) Planch. and *Helianthus annuus* L. In *Syringa*, the callus was obtained from the cambial region of the stem by well-established techniques (Gautheret, 1942; Morel,

1948). All the experiments were completed from a single clone of the callus. Callus for the other two species was obtained from sections of the stem (Gautheret, 1942; Morel, 1948).

Syringa callus grows well *in vitro* on the following medium: —

Knop's solution ¹	500 cc.	Cysteine	10 mg.
Double distilled water	350 cc.	Autoclaved coconut milk.	
Minor elements ²	1 cc.	15%	150 cc.
Ferric citrate	10 mg.	Vitamin-free casein	
Sucrose, 5%	50 g.	hydrolysate	1 cc.
Vitamin B mixture ³	1 cc.	Agar, 1%	10 g.

¹ As modified by Gautheret (1942; Nitsch, 1951).

² Stock solution made up according to the formula of Nitsch (1951) with the addition of 25 mg. of Co Cl₂.

³ The composition of the Vitamin B mixture employed is as follows: — Thiamin hydrochloride 1.0 mg./cc.; Pyrodoxin 1.0 mg./cc.; Nicotinic acid 5.0 mg./cc.; Riboflavin 0.5 mg./cc.; Calcium pantothenate 5.0 mg./cc.; Folic acid 0.1 mg./cc.; Biotin 0.01 mg./cc.; Choline chloride 1.0 mg./cc.; Para-amino-benzoic acid 0.5 mg./cc.; Inositol 10.0 mg./cc.

The same medium fosters the growth of *Parthenocissus* and *Helianthus* cultures, except that certain changes in sucrose (to 6%) and in coconut milk (to 5%), respectively, seem to improve their growth. Callus cultures grow well enough to need transferring at least every three months.

Apices of *Syringa* shoots, usually with three to five pairs of leaf primordia, are prepared for grafting by cutting the base into a wedge, the whole being perhaps 3 to 5 mm. long. A piece of lilac callus is removed from its culture tube into a petri plate, and a V-shaped cut is made into the top of the callus, the sides of the V being kept at about the same slant as those of the wedge-shaped scion to be grafted. Into this cut is put enough agar, or nutrient medium, as called for by the design of the experiment, to fill it.⁴ The prepared apex is then pushed into this agar or nutrient agar medium, due regard being given to the orientation of the slanting sides of the apex and of the corresponding walls of the V-shaped cut. When firmly in place, the grafted apex-on-callus is planted in a new tube of medium and left to grow (FIGS. 1-3). In some experiments, no apex is planted in the V-shaped cut; the medium in the cut is characteristically replaced at intervals.

Large pieces of callus with grafted apices are prepared for embedding and sectioning by gashing the surfaces to ensure penetration of reagents into the limited intercellular spaces of the massive callus and to ensure better aspiration in the killing and fixing agent. Craf III is employed for this purpose on a modification containing a higher concentration of acetic acid which seems to give less shrinkage of cells. Materials are embedded in Tissue Mat, sectioned, stained, mounted, and photographed by standard techniques.

⁴ So far as the author knows, this technique was first published by Camus (1949). To Dr. G. M. Morel, a co-worker at that time, who knew of and showed him the technique before Camus' publication had been received, the author owes sincere thanks.

GRAFTS OF APEX OF SYRINGA ON SYRINGA CALLUS

Apices of growing lilac branches show visible signs of growth within a week after being grafted into lilac callus. If the medium contains basic mineral salts, minor elements, 2% sucrose, and a low physiological concentration of an auxin (0.1 mg./l. of naphthaleneacetic acid), the callus and the scion grafted into it respond slowly (FIGS. 1, 2). If then transferred to a coconut milk (15%–20%), casein hydrolysate mixture, B-vitamin mixture, sucrose (5%) medium (FIG. 3), growth is rapid in both callus and grafted scion. In fact, within two to three months the scion often develops roots (FIG. 3, right), and the new plant becomes independent of the callus host.

In all, over the past five years, more than 150 grafts of lilac apices on lilac callus have been made, the medium studied and improved, and many resultant growths have been sectioned and studied.⁵

It is interesting, though not unexpected, that the medium proving best for lilac apices by themselves is also that most beneficial for the growth of lilac callus and for scions of lilac grafted into that callus. When two or three apices are grafted into the same callus (FIG. 1), characteristically they all start growing, but, more often than not, one of these outgrows the others; in such cases the effects of the competition become increasingly apparent with time (FIG. 3).

A histological investigation of graft unions shows a well-integrated system. It is difficult to tell from older, established grafts how the union was initiated. A study of young cases suggests no uniformity of behavior. Sometimes cell proliferation occurs on the flanking surfaces of the V-shaped scion; at other times early activity seems largely to be from the sides of the incision in the callus host. The soundness of the technique used by Camus is found in the effect of the agar, whether alone or containing nutrient medium, on the cut cell walls; these are never dry, and seem to be no deterrent to good graft unions. When the grafts have been firmly established and such space as may have existed in the V-shaped cut between host and scion has been filled by cell proliferation, a kind of interdigitation is evident in which outgrowths of either may invade the other. This is especially evident in cases in which lobes from the scion displace neighboring shoot tissue — witness the large bifid-appearing lobe (FIG. 4) below and to the left of the scion, and another at the upper left. The lower lobe is not of proven connection in the figure, but in neighboring sections the connection is very evident.

In order to illustrate a common set of reactions to the influence of the grafted apex, a typical series is illustrated by representative transverse sections of low magnification (FIGS. 5–12), and by enlarged views of critical parts of these sections (FIGS. 13–18). The illustrations have been selected from a study of a 54-day-old graft which had two or three pairs

⁵ I want to pay tribute to past students who have had a share in this work, especially Dr. Carl Price and Mrs. Eleanor Gossard Shore.

of leaves left on the apex when dissected for grafting. Originally two apices were grafted into this callus; when killed and fixed the callus was cut in two pieces, each with its scion; both pieces were sectioned and studied, and essentially the story for one is the story for both. In fact, this story would have done for others grown on any medium if the same non-auxin-containing agar was used to fill the cut before the scion was planted. It will be noticed, however, that all proliferation throughout the callus was general and abundant, even as it was extensive and important in the scion itself. It is believed that the description which follows will enable the reader to understand trends and interpretations to be commented on later in the text. TEXT-FIGURE 1 will be helpful. The scion is established in the top 3 mm. of this half of the callus, which is about 12 mm. thick. The cross section pictured below is near the 2 mm. level.

The first section (FIG. 6) is less than 1 mm. below the surface of the callus. The V-shaped cuts are indicated along the nearly horizontal edges of the scion; the nearly vertical edges still are epidermis-covered and therefore uninjured. The vascular cylinder was injured by the cutting preliminary to grafting, but in the proliferated cell masses of the flanks of the scion it has more or less reestablished itself. Certain vascular strands can be seen in the host callus along the cut sides.

Some 500 μ lower (FIGS. 5, 13), the vascular cylinder of the scion has become larger, instead of smaller. An examination of the cylinder at the higher magnification (FIG. 13) suggests an explanation for this change in size. Reactivation of cell division in the pith is supported by the radial rows of cells abutting on the inner sides of the xylem. In fact, this radial extension of the pith has become so pronounced that pressures have disrupted the pith, the newly proliferated scion tissue on the lower flank, and even the callus tissue beyond the limits of the scion. The borders of the scion can be more or less identified by the black-staining remains of the agar placed earlier in the incision. It is noteworthy that the tear seems to have become somewhat filled up with proliferated cells. Subsequent enlarged sections will show this same phenomenon.

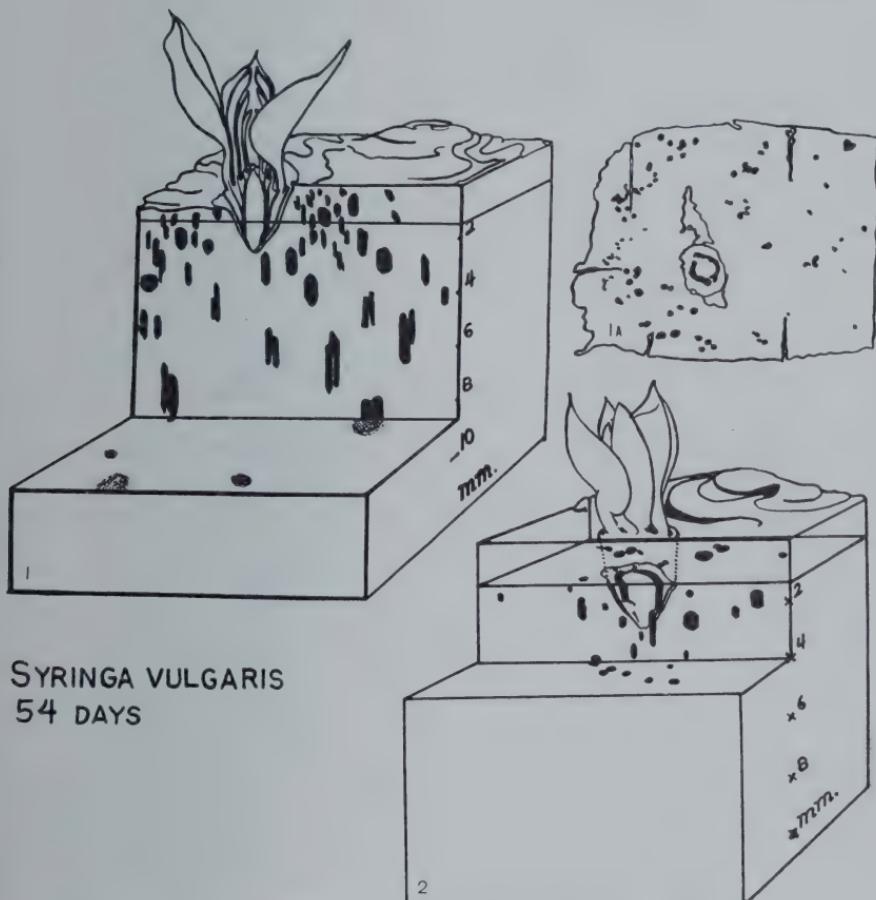
In the next section, almost at the 2 mm. level of FIG. 2 (FIGS. 7, 14, 15), the changes of the next 300 μ can be recognized. The arc of vascular tissue on the right of the scion (FIG. 7) is now of two parts. Some of the extensive, radially organized pith has become secondarily thickened and lignified as xylem. For example, the left-hand vascular arc is shown enlarged in FIG. 15. Here one large cell, somewhat oblique, is a vessel segment — marked X — the porous perforation showing clearly at one end. Numerous other elements in this and the neighboring radially arranged rows are circular-bordered in pitting, though not too clear at this magnification.

Mention should be made of the obvious vascular strands in the callus regions near to both flanks of the scion (FIG. 7); these were less numerous in earlier sections (FIGS. 5, 6) but were represented there. (Note TEXT-FIG. 2.)

At approximately 500 μ further (FIGS. 8, 16), more reduction in the vascular tissue of the scion is evident. The split in the pith and adjacent

flanking tissue of the scion stands out, and radial organization of the pith is still obvious, especially on the left (FIG. 16). The indefinite boundary between the tightly knitted scion and the host callus is scarcely to be told on the lower flank in this figure except for the black-stained agar and the seeming contrast in size of cells.

In FIGURE 17, 20 μ lower than FIG. 8 or 70 μ lower than FIG. 16, the reduced vascular tissues in the scion are represented by two circular strands.



SYRINGA VULGARIS
54 DAYS

TEXT-FIGURE 1. A stereogram of a piece of lilac callus into which was grafted an apex of lilac bearing 2 or 3 pairs of leaf primordia. The incision was filled with 1% agar plus 0.05 mg./l. n.a.a. This drawing is made from a study of a series of transverse sections, when the graft-callus had grown for 54 days. TEXT-FIGURE 1A shows a transverse section at about the 2 mm. mark.

TEXT-FIGURE 2. A second stereogram of another graft showing more clearly the relation of vascular strands in the graft and in the scion below, indicating a near continuity on the right-hand side; in this graft, no auxin was put in the agar placed in the incision. Note the scattered strands in both text-figures.

Radially organized pith still can be detected on the left side. By 100 μ lower, the smaller strand has disappeared, leaving a stretch of radially organized scion parenchyma. In FIGURE 9, about 150 μ lower, the remaining circular vascular strand is much reduced, the only recognizable scion tissue being the small, circular, black agar-delimited area around this strand. The remainder of the section is of callus tissue, with some vascular strands.

About 3.0 mm. below the surface of the callus, or about 0.5 mm. below the bottom of the scion (FIG. 10), a new central bundle can be recognized, situated almost exactly in the position of the round strand (FIGS. 17, 18) which disappeared and was replaced a few sections later (TEXT-FIG. 2) in the callus. This new strand can be followed down for a considerable distance in the callus (FIG. 11) until it is no longer recognizable in the medley of strands present (FIG. 12) a full millimeter below.

Even though vascular strands become increasingly evident at varying distances below the scion, the number diminishes some 6 mm. below the surface or about 3 mm. down from the lower extremity of the scion (TEXT-FIG. 1).

A study of this series and many others of similar kind seems to allow the following inferences: —

1. A scion grafted into callus with no auxin in the agar filling the incision before grafting, whether it is present or not in the sterile medium upon which the apex-callus is grown, tends to (a) produce new vascular tissue in its own proliferated pith tissue, and (b) to stimulate the mitotic activity, which gives rise to nests or short columns of cells in the callus. These columns become organized into vascular strands, often of short vertical extent. Frequently these strands can almost be considered as continuous with those in the scion.

2. The scattered strands of the callus are most numerous below or on the lower flanks of the scion not at greater distances away.

3. The strands, when organized so that mature cells are present, contain lignified, pitted xylem elements, often perforate. No conducting phloem cells have been recognized. Macerations must be carried out, however, before their absence can be made certain.

4. Organization of vascular strands was obviously incomplete when the experimental studies were stopped. Cultures must be maintained longer to learn what further development may produce. Clearly, the characteristic continuous vascular cylinder of the lilac stem is not formed in the callus. Equally clearly, it is hard to picture any relation between organization of vascular strands and conduction.

EFFECTS OF AUXIN-TREATED INCISIONS IN CALLUS

In certain experiments, we used nutrient agar in the incisions instead of plain agar. These nutrient agar media vary in auxin content. In some, we added definite concentrations of synthetic auxins, in others varying amounts of autoclaved coconut milk, with large but unknown concentrations of auxins (Nitsch, 1955). It is evident from these studies that the

concentration of auxin in the incision agar, however added, limits the differentiation of vascular strands around the grafted scion; nor is there any mitotic activity found in the pith of the scion. Rather, vascular strands develop at varying distances from the axis of the scion, these distances having a direct relation to the concentration of auxin present. If higher concentrations are employed in the incision agar, the vascular strands form well out toward the periphery of the callus.

Because auxin produced by the apical meristems, leaves, etc., is significant in the production of vascular tissue in the characteristically parenchymatous callus, it was resolved to leave the scion out completely and study the effects of variations in incision-auxin level alone.

When into an incision was put agar containing 0.25% of naphthalene-acetic acid (n.a.a.) in lanolin and when the whole callus was grown on the best medium now known for *Syringa*, 15% autoclaved coconut milk with its naturally occurring auxin, casein hydrolysate, and 5% sucrose, the callus grew well (See Material and Methods). After four and a half months of active growth, sections showed no vascular tissue anywhere (FIG. 21). This absence of vascular strands is what one characteristically finds in *Syringa* callus on all media studied.

By contrast, when the incision was provided with nutrient medium in agar containing the same content of auxin as indicated above, i.e., 15% autoclaved coconut milk, active arcs of extensive cell proliferation occur in the callus (FIG. 19), which give way to vascular strands.

In another instance of interesting response, the incision was filled with n.a.a. in agar in a concentration of 5 mg./l.; the callus was subsequently grown on the standard medium containing 5% sucrose, vitamin B mixture, 15% autoclaved coconut milk, and 1 cc./l. of casein hydrolysate with the usual mineral-agar background. Great activity was found just within the periphery at the end of thirty-one days (FIG. 20). Material kept longer gives indication of vascular strands being organized in this rectangular, cambial-like zone, as is already suggested in the upper part of FIG. 20.

It would appear that auxin in the incision agar in the range of physiological concentrations without being supplemented by a growing scion can produce those conditions which favor the incidence of vascular tissue in the callus.

DISCUSSION

The apical meristem of the shoot system has at least three well-recognized functions. It adds new cells to the apices. It gives rise to the primordia of new leaves and buds. It plays a part in controlling biochemically the organization of the stem behind it (Ball, 1946, 1948, 1949, 1951, 1952a, 1952b; Wardlaw, 1944, 1947, 1949, 1950, 1952; Wetmore and Wardlaw, 1951; Jacobs, 1952, 1954). Little is known of how these organizational changes are brought about. Evidence has accumulated to suggest that an auxin plays a limiting role in the differentiation, especially so far as it relates to xylem. These auxin effects, so far as known, have recently been

reviewed by Jacobs (1952, 1954). He concludes that in *Coleus* (1952) much more of the auxin has its origin in the young leaves than in the apical meristem itself, leaf number two being the largest contributor. In consequence, once carbohydrate shortage in the upper regions of the plant has been cared for,—this being a second limiting factor as he envisions it—xylem differentiation is initiated, and in the angiosperms at least, in a basipetal direction in keeping with an auxin gradient. Known facts accord with this interpretation. He adds to the earlier work of Simon (1930) and of Kaan-Albest (1934) in finding that there is in this group of plants also a slight and slow acropetal differentiation of xylem as well as that in a basipetal direction. Perhaps a major contribution is in his more recent study (1954). Here he reports that there is in a developing internode a lesser acropetal movement of auxin than basipetal, to a ratio of about 1:3. Broadly, this is in keeping with the contrast between the two aggregates of differentiated xylem, the basipetally developed portion being about three times as much as that developed acropetally.

In the present studies, mitotic activity begins on the cut surfaces of both callus host and the grafted apex within a few days following the operation. In those examples in which the apex is put in auxin-free agar in the incision, the surface activity is followed by a rib meristem-like series of mitoses on either side of the pith, oriented such that the ribs are at right angles to the vascular strands. This development occurs only with the opening of the grafted bud and essentially at the same time as the activity on the surfaces at the graft union. That some of this newly formed, regularly and radially arranged pith, especially on and near the cut flanks of the scion, should become vascular is noteworthy. The implication can only be that something in the experimental procedure has either removed the limitation which kept pith tissue stable or has stimulated it to divide again in orderly fashion. This permits or promotes the next stage from which, as might be expected in lilac, ultimately are produced crowded, circular-bordered, pitted vessel segments with porous perforations in oblique end walls (FIG. 15). The elements are shorter than they are in normal xylem of lilac. One cannot know from these specimens, which were grown as grafts for only fifty-four days, what might have happened had they been grown longer. The experiment must be tried again and for longer periods. For the present, it must be pointed out that no phloem has been detected in the new tissue of this nor like grafts. This seeming absence might be due to failure to recognize it, since careful diagnosis is necessary for identification of phloem either by special stains (Cheadle, Gifford and Esau, 1953) or by maceration. It is proposed to follow the present study with others in which both techniques are invoked.

Soon after the rejuvenation of the pith, and with the closing of the agar-filled incision by the completed graft union, vascular strands begin to appear in that part of the callus flanking the V-shaped cuts, not far from the incisions. The earliest strands arise on the flanks, about three-quarters of the way down the V-cut, and, once initiated as centers of mitotic activity, develop basipetally, quickly acquiring vascular elements of pitted xylem.

These are followed by other strands below the scion almost in continuity with those of the uncut ends. Strands also appear in the callus near the lower edges of the cuticle-covered epidermis of the ends. Later, more strands appear in the callus on the flanks, even farther out and lower down than those reported above (TEXT-FIG. 2). At the time that experiments were stopped — and a 54-day period was the longest any were maintained in culture — the strands were all of short vertical extent. Their ultimate length and possible duration of development are unknown.

It is important to realize that vascular strands in the positions which many of these occupy and with no more continuity than they exhibit could have little significance as water-conducting xylem. One cannot avoid pondering this fact in terms of the pattern of development in normal stems. Is the solution of this problem of the differentiation of xylem in the cylindrical or near-conical axis of the shoot to be found in the fact that continuing strands of elongating procambial cells are preferred paths for auxin movement? If carbohydrates carried by phloem represent a second necessity for xylem differentiation, then one can recognize the significance of the characteristic pattern of phloem differentiation preceding xylem differentiation at any level (Jacobs, 1954). Given carbohydrate, through differentiated phloem elements, and auxin in adequate amounts, it appears that these factors are no longer limiting to xylem differentiation. As it is likely that the favorable concentrations of auxin and carbohydrate are likely to be in the procambium, it is to be expected that xylem formation should be associated with the presence of phloem.

Importance is attached to the fact that vascular strands can experimentally be somewhat generally allocated to regions of the callus. If, instead of a 1% agar as the medium to fill the cut before the scion is inserted, the agar contains a synthetic auxin in known concentration in the physiological range, the vascular strands formed in the callus reflect the auxin concentration. With a concentration of 1 mg. per l., the strands occur only towards the outside of the callus, very few being found near the scion. With 0.01 mg. per l. in the agar placed in the incision, few strands occur near the periphery of the callus — in pieces approximately 1 cm. on a side; they tend to be aggregated on the lower flanks and below the scion. In a broad way, the number and distribution of the strands is dependent upon the concentration of the auxin, at least for either naphthaleneacetic acid or indole-3-acetic acid, the only auxins tried.

When the usual V-shaped cuts are made in the callus, these cuts filled with an auxin-agar mixture, but no apex inserted, results are obtained not dissimilar to those with the apices. A low concentration of auxin (FIG. 21 with 0.25% n.a.a. in lanolin) gives in four and a half months no strands at all. By contrast a medium containing 0.05 mg. per l. of n.a.a. + 15% autoclaved coconut milk, with its high concentration of indole-3-acetic acid, and 5% sucrose (FIG. 19) produces strands scattered in the callus. Few to none of these, however, are found in proximity to the cut, even though the auxin-agar was only replaced once during five and a third months. Again, when 5 mg. per l. of n.a.a. in 1% agar is put into the

incision, a cambial-like zone, very often found in similar cases, is produced toward the outside of the callus, which then resolves itself into strands of xylem, as can be seen (near the upper left, FIG. 20).

In summary, it seems clear that the findings from the early and beautifully planned experiments of Camus (1949) and the more recent and equally significant studies of Sinnott and Bloch (1944) and of Jacobs (1952, 1954) are further supported by the present investigations. It is clear that an auxin placed in or near the top of a callus can make the difference between the formation and the non-formation of vascular strands in which at least xylem differentiates. The role of sugar, as suggested by Jacobs, is not absolutely confirmed, though circumstantial evidence points to its probability. An important problem remains. Why do physiological concentrations of auxin in the agar medium foster the growth of *Syringa* callus *in vitro* but are not effective in the formation of vascular strands in the callus? Yet the same concentrations used in incisions on the upper surface of the agar are accompanied by the appearance of strands. This would seem to suggest a polarity to the callus, as was reported by Gautheret (1940) for carrot tissues, even when isolated from the carrot, and (1941) for endive root tissues. The general handling of callus tissues after a few transfers suggests little polarity, as indicated by a preferential absorption of auxin from the medium. One reason thus from the fact that growth appears very uniform in pieces planted with little or no regard to their orientation with relation to the original plant. Experiments will be made to investigate the question of polarity of lilac callus in its relation to auxin transfer when initially grown and after varying numbers of passages to new media.

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EXPLANATION OF PLATES

PLATE I

FIG. 1. Habit of *Syringa* apex grafted into *Syringa* callus, 7 weeks old. Graft incision filled with agar containing 2% sucrose and 0.1 mg./l. n.a.a.

FIG. 2. Habit of 19-week, 5-day-old graft of *Syringa* apex into *Syringa* callus. Agar mixture used in graft incision as above.

FIG. 3. Habit of 8.5-months graft of *Syringa* apex into *Syringa* callus. The graft was planted on the medium of FIGS. 1 and 2; at the end of 6 months it appeared about as in FIG. 2. Upon transfer to a medium containing 20% autoclaved coconut milk, casein hydrolysate (1%), it grew to the pictured, internode-bearing plant, rooted (see 2 short roots on right-hand plant) in about 2½ months. Note control apex in the middle, not grafted.

PLATE II

FIG. 4. Longitudinal section of callus-graft union of 5-weeks-old graft. Note black-stained agar around the base of the scion. Two lobes of the scion are shown on the left, the upper cut almost in median plane, the lower not shown in direct connection with the main body of the base of the scion. $\times 10$.

FIG. 5. Transverse section of scion-graft union of a 54-day graft grown on a dextrose, yeast-extract medium with thiamin and cysteine, but no coconut milk nor synthetic auxin; 1% agar used in the incision. Section almost 1.5 mm. below surface of callus-graft union. Note upper and lower flanks of scion are along cut edges of wedge-shaped scion base. The side surfaces of the scion are epidermis-covered. $\times 11.6$. (This section is about 500 μ below FIG. 6, but through an error was mounted out of order. The section labelled FIG. 6 and there described is actually FIG. 5 and that described as FIG. 5 is FIG. 6.)

FIG. 6. Transverse section about 500 μ above FIG. 5. Note increased diameter of vascular cylinder, due to radial multiplication of pith cells (See FIG. 13). $\times 11.6$.

PLATE III

FIG. 7. Transverse section about 300 μ below FIG. 6. Note the arc of the vascular cylinder on the right is disrupted; radial organization of the pith is especially prominent on the left. Note the extra vascular strands on both flanks, above and below. See FIGS. 14, 15 for enlargements from section close to this one. $\times 11.6$.

FIG. 8. Transverse section about 500 μ below FIG. 7. Note the narrowed wedge of the scion; two strands of vascular tissue are left, much decreased in size. Agar is irregularly distributed. As epidermis disappears on right, note appearance of strands in callus. See FIG. 16 for enlargement. $\times 11.6$.

FIG. 9. Transverse section about 150 μ below FIG. 8. The left vascular strand of scion has disappeared, the right, almost so. A small black agar-contained area with remains of right vascular strand is obvious. Some strands are visible in the callus. $\times 11.6$.

PLATE IV

FIG. 10. Transverse section over 0.5 mm. below FIG. 9. Right-hand arc of cylinder has disappeared, but it has been replaced by another almost below it. See TEXT-FIG. 2. Strands in the callus are more pronounced. $\times 11.6$.

FIG. 11. Transverse section about 0.25 mm. below FIG. 10. Note continuing central strand and enlarged strands in the callus. $\times 11.6$.

FIG. 12. Transverse section about 1.0 mm. below FIG. 11. Note increasing prominence of the numerous strands. $\times 11.6$.

PLATE V

FIG. 13. Enlarged view of scion of FIG. 5. Note rows of new cells in pith on both sides; these radial rows have become extensive enough to displace laterally the original vascular tissue, tearing the pith and cortex of the scion and the adjacent callus. $\times 55$.

FIG. 14. Enlarged view of scion of section 40 μ above FIG. 7. Note radial rows on either side of tear in pith. $\times 55$.

FIG. 15. Enlarged view of right-hand part of vascular cylinder of FIG. 14. Note oblique vascular elements in upper part of radial rows; element marked X shows vessel perforation; neighboring elements in side view show crowded, circular bordered pits. $\times 67$.

FIG. 16. Enlarged view of scion from section 50 μ above FIG. 8. Note reduction of arcs of vascular cylinder; radial rows and tears in pith still obvious. $\times 50$.

FIG. 17. Enlarged view of much smaller scion 20 μ below FIG. 8. Note rapid reduction in extent of vascular strands in the 70 μ between FIG. 16 and FIG. 17. Radial organization of pith still present. Note limits of grafted scion as indicated by black agar lines. $\times 50$.

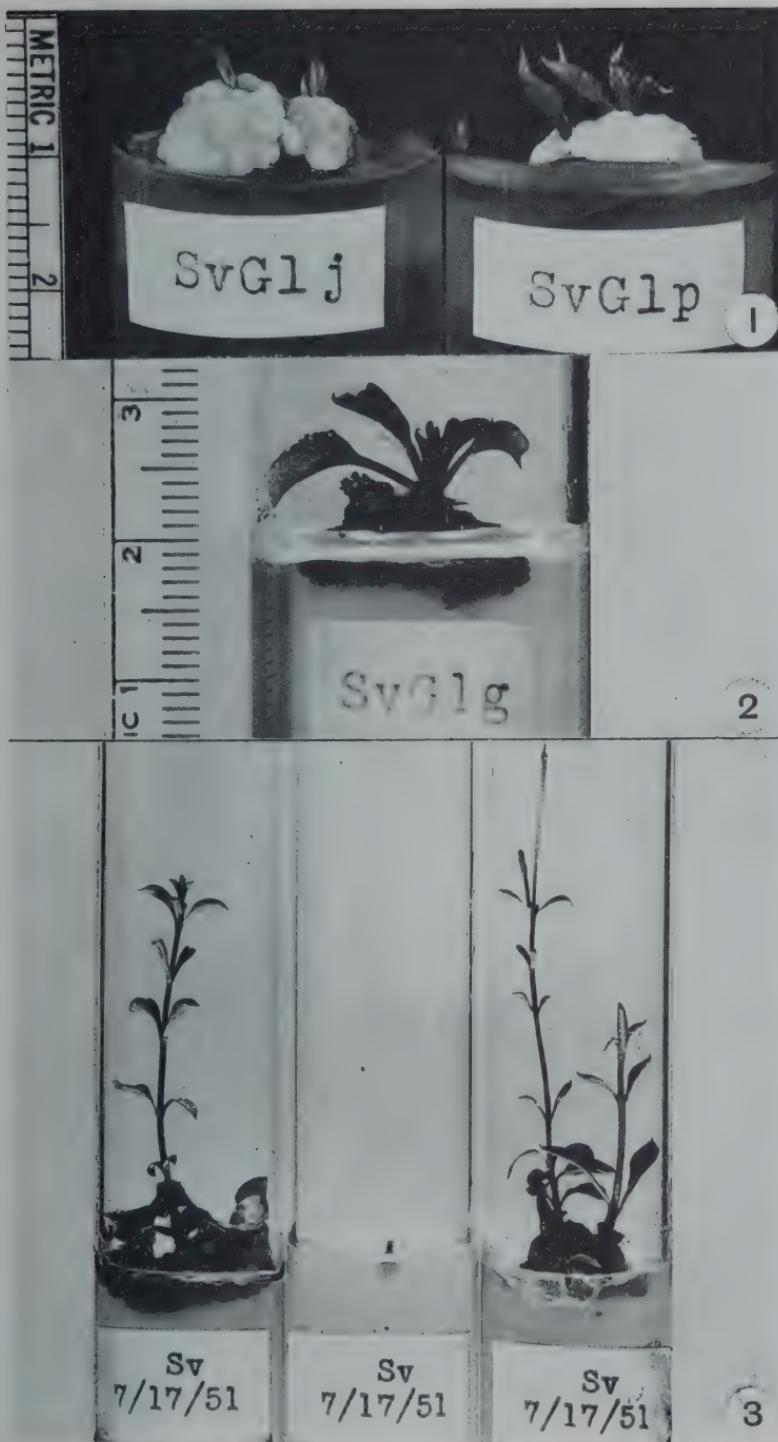
FIG. 18. Enlarged view of transverse section of scion 90 μ below FIG. 17 (or 40 μ above FIG. 9). Note left-hand strand has disappeared leaving the large proliferated parenchymatous mass at base of scion. The right-hand strand is present, circular in outline. $\times 45$.

PLATE VI

FIG. 19. Transverse section of callus cut through remains of V-shaped cut after 5 1/3 months. Cell proliferation has almost filled the incision, only irregular bits remaining. Little of the agar is visible, though it was replaced once. The agar contained 15% coconut milk and 5% sucrose. Note extensive cell proliferation midway out in callus which has given way to vascular tissue. $\times 4.2$.

FIG. 20. Transverse section of 31-day callus after incision in upper surface was filled with agar containing n.a.a. in a concentration of 5 mg. per l. and 5% sucrose. Mixture replaced once. Note absence of vascular strands near incision and the rectangular cambial-like layer near the periphery. This layer begins to show strands in the upper left. $\times 10.4$.

FIG. 21. Transverse section of a 4 1/2-months' callus grown on a favorable medium with an incision in the top filled with 0.25% n.a.a. in lanolin which was replaced once. Note the absence of vascular strands over the whole callus; auxin diffuses much more slowly from lanolin than from auxin.

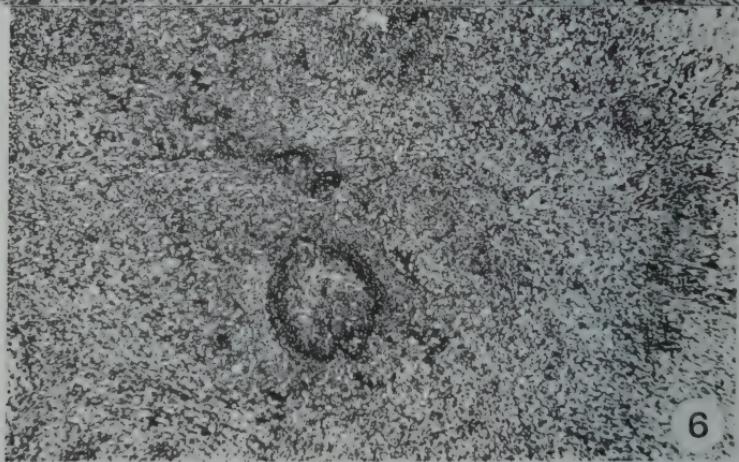




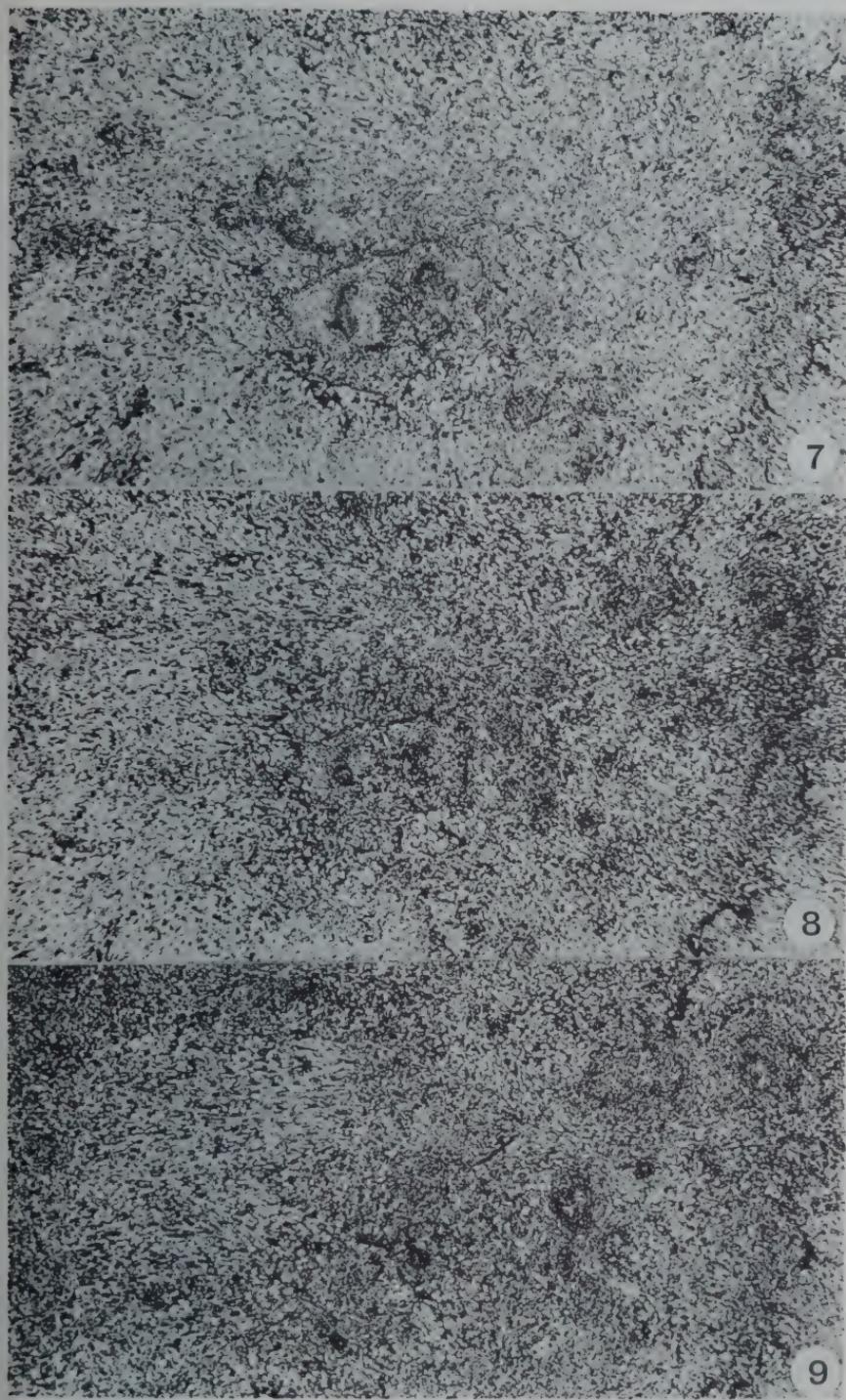
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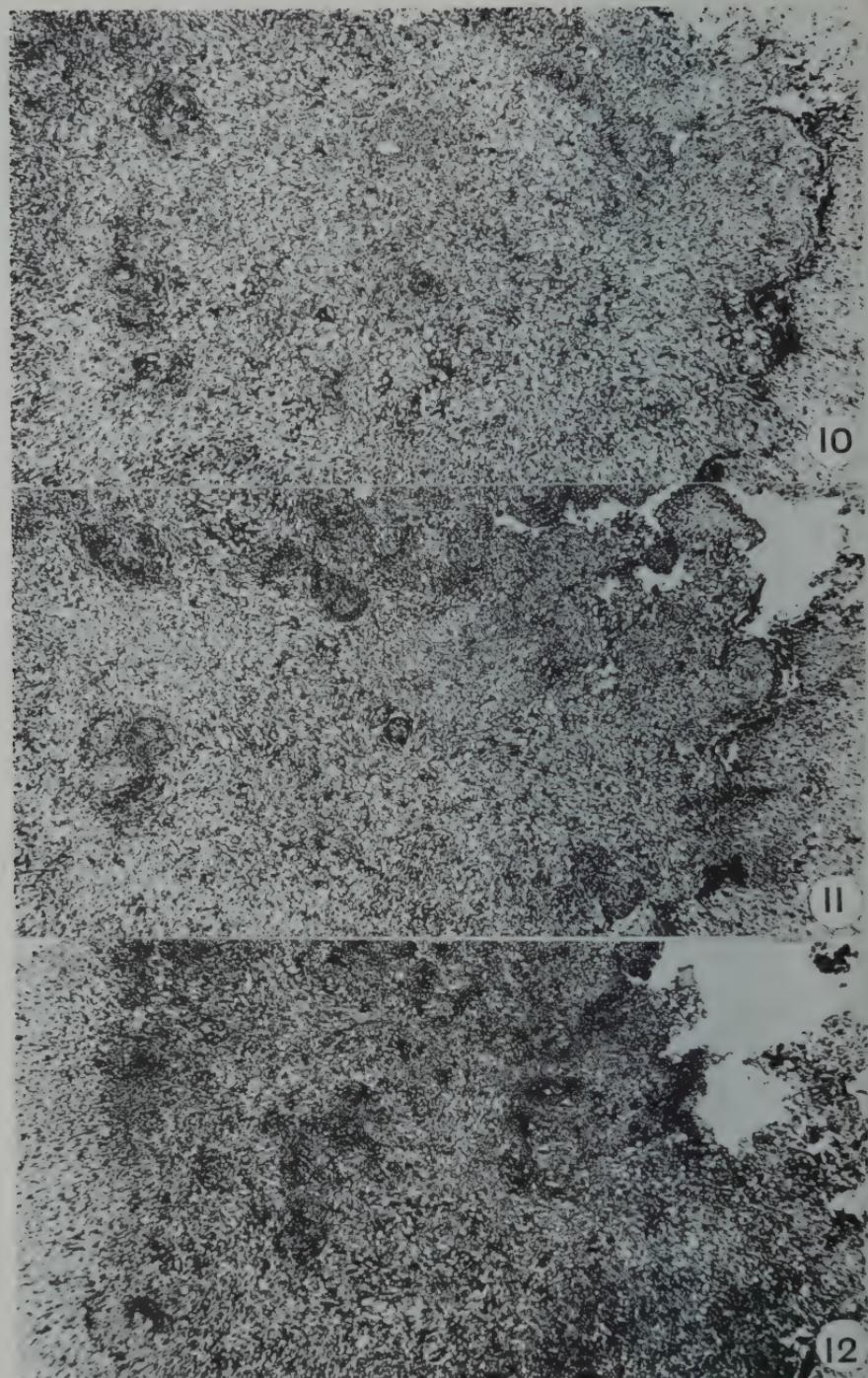


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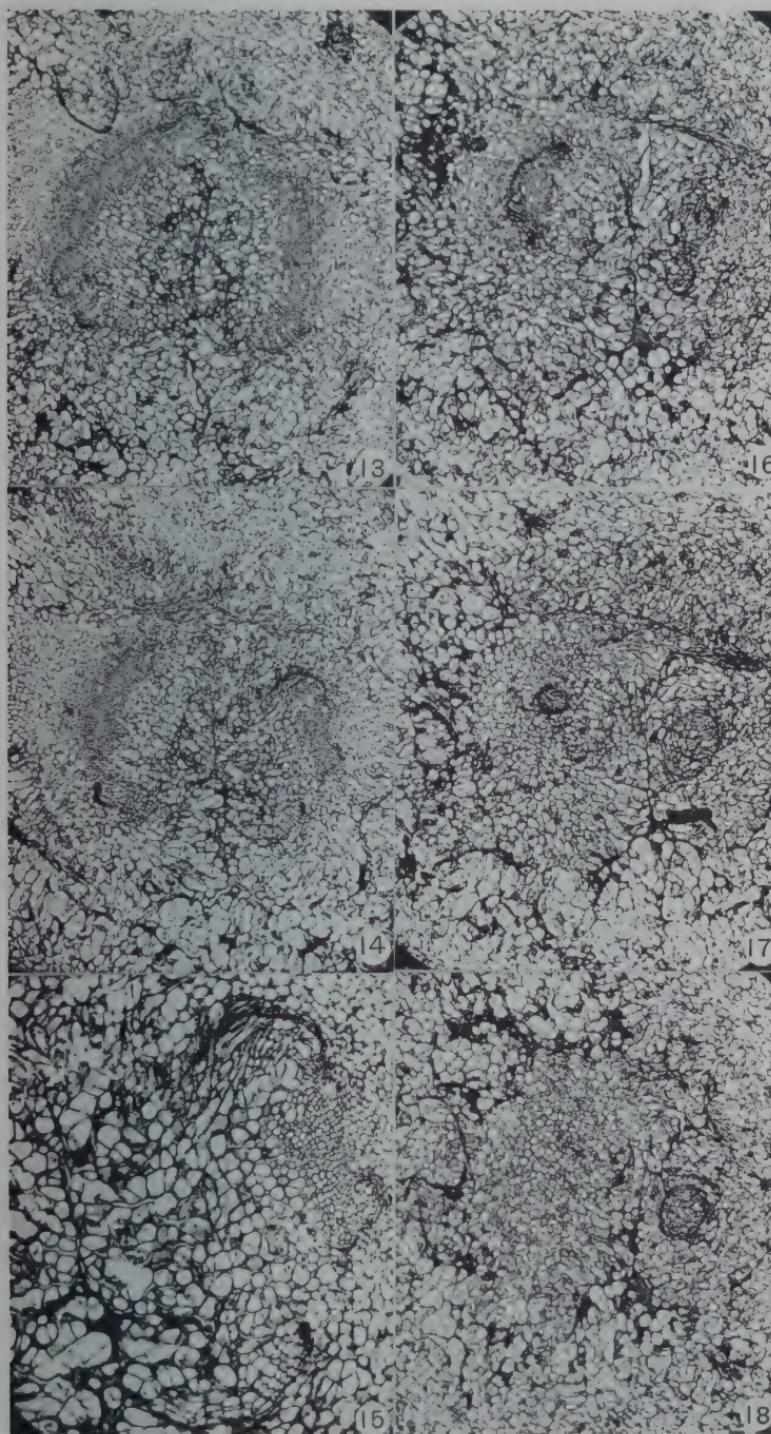


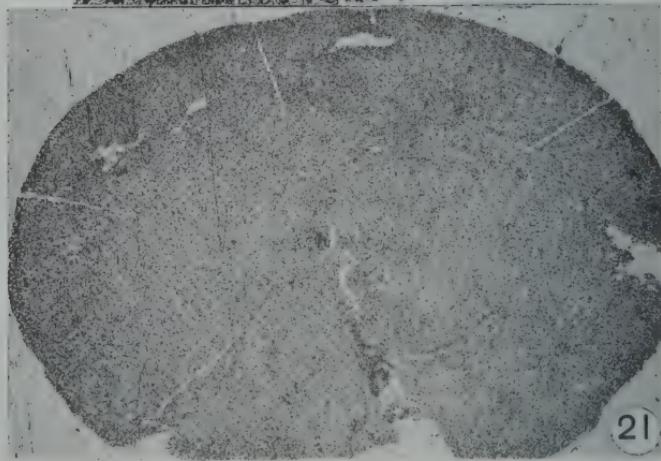
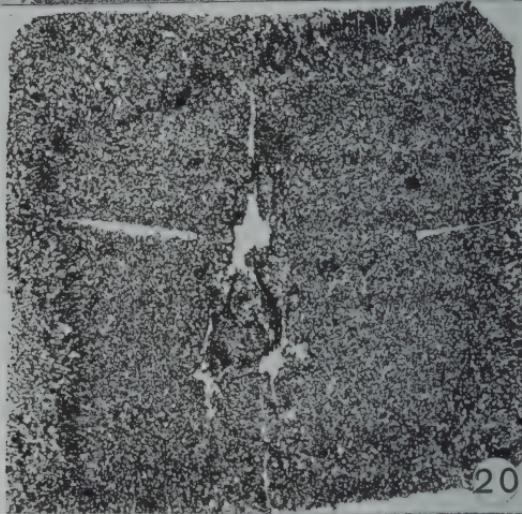
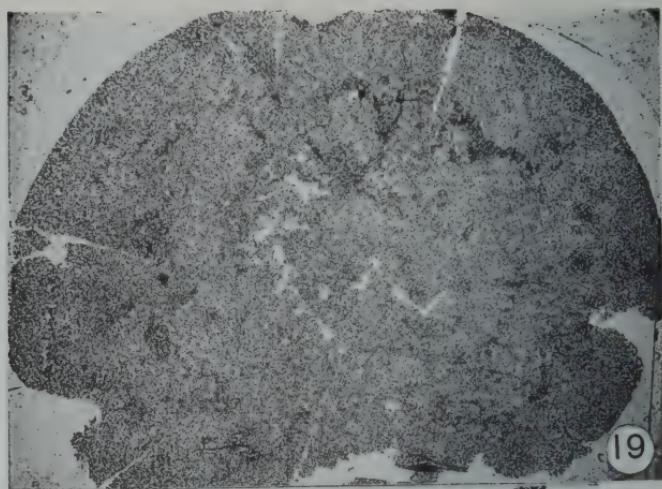
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CONTENTS OF NO. 4

A MONOGRAPH OF THE GENUS PHILADELPHUS (Continued). By <i>Shiu-ying Hu</i>	325
STUDIES ON THE PROGENY OF TRIPLOID PHILADELPHUS AND FOR- SYTHIA. With one plate. By <i>Dexter R. Sampson</i>	369
GEOGRAPHICAL DISTRIBUTION OF THE EUPOMATIACEAE. By <i>A. T. Hotchkiss</i>	385
FURTHER NOTES ON THE WEEDS AND INTRODUCED PLANTS OF FIJI. By <i>William Greenwood</i>	397
THE DIRECTOR'S REPORT	403
BIBLIOGRAPHY OF THE PUBLISHED WRITINGS OF THE STAFF AND STUDENTS, July 1, 1954–June 30, 1955	428
STAFF OF THE ARNOLD ARBORETUM, 1954–1955	431
INDEX TO VOL. XXXVI	433
TITLE-PAGE AND TABLE OF CONTENTS	i–iv

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A MONOGRAPH OF THE GENUS PHILADELPHUS *

SHIU-YING HU

Series 5. *Delavayani*, ser. nov.

Philadelphus subg. II. *Euphiladelphus* sect. 4. *Stenostigma* ser. 5.
Delavayani, ser. nov.

Philadelphus sect. *Stenostigma* subsect. *Satsumani* Koehne in Mitt. Deutsch.
Dendr. Ges. 1904 (13): 82. 1904, pro parte.

Philadelphus sect. *Poecilostigma* subsect. *Gemmata* Koehne in Mitt. Deutsch.
Dendr. Ges. 1906 (15): 51. 1906, pro parte.

TYPE SPECIES: *P. delavayi* L. Henry.

Frutex ramulis griseis, raro castaneis, cortice clauso; foliis ovatis vel ovato-lanceolatis, subtus plerumque dense pubescentibus, inflorescentiis 7-, 9-, raro 5- vel 21-floris; hypanthiis glaberrimis, saepe pruinosis, purpurescentibus; corolla disciformi vel subcampanulata, raro cruciformi; staminibus 25 usque 35, disco et stylo glabris; stigmatibus linearibus, dorsalibus; capsulis obovoideis; seminibus breviter caudatis.

Both geographically and morphologically this series is intermediate between the western Himalayan series *Tomentosi* and the northern Chinese series *Pekinense*. Members of this series occur in southwestern China between Long. 98° and 102° E. and Lat. 26° and 30° N. They are characterized by their pubescent leaves, glabrous hypanthia, green and purplish calyx, linear and abaxial stigmata and short-caudate seeds. The distribution of the species in this series is shown in map 5.

KEY TO THE SPECIES

A. Hairs on the lower leaf-surface villose; corolla disciform or rarely cruciform, generally 3 cm. or more in diameter. 32. *P. delavayi*.
AA. Hairs on the lower leaf-surface strigose; flowers small, the corolla campanulate, less than 3 cm. in diameter. 33. *P. purpurascens*.

32. *Philadelphus delavayi* L. Henry in Rev. Hort. 1903: 13, fig. 3. 1903.
— Koehne in Mitt. Deutsch. Dendr. Ges. 1906(15): 51. 1906. —

* Continued from volume XXXVI, page 109.

Schneider, Ill. Handb. Laubh. 1: 370. 1905.—Stapf in Bot. Mag. 149: pl. 9022. 1924.—Diels in Notes Bot. Gard. Edinb. 7: 106. 1912.—Léveillé, Cat. Pl. Yunnan 255. 1917.—Rehder, Man. Cult. Trees Shrubs 275. 1927; ed. 2, 269. 1940; et Bibl. Cult. Trees Shrubs 192. 1949.—Hand.-Mazz., Symb. Sin. 7: 438. 1931.—Chen, Ill. Man. Chin. Trees Shrubs 372, 1937.—Merr. in Britt. 4: 66. 1941.—Bean in Chitt., Dict. Gard. 3: 1546, fig. [1]. 1951.



TYPE: *J. M. Delavay* 2871 (Muséum Nat. Hist. Nat. Paris).

Shrub 2–4 m. high; bark of the second year's growth grayish brown, rarely gray or castaneous, closed, with transverse cracks; current year's growth glabrous, pruinose. Leaves ovate-lanceolate or ovate-oblong, those on the sterile shoot 5–14 cm. long, 2–7 cm. wide, those on the flowering shoot 2–8 cm. long, 2–5 cm. wide, serrate, rarely subentire, rounded or obtuse at the base, acuminate, rarely acute at the apex, the acumen 5–20 mm. long, uniformly setose above, densely villose beneath, the trichomes compressed. Inflorescences 5-, 7-, or 9-flowered, rarely up to 21-flowered,

the lower pairs in the axils of normal leaves, sometimes cymose; pedicels glabrous, 5–10, rarely up to 13 mm. long, hypanthium and calyx glabrous, pruinose, green tinged with reddish brown; sepals ovate, 6 mm. long, 4 mm. wide, acute at the apex; corolla disciform, 2.5–3.5 cm. across, the petals suborbicular, 1–1.5 cm. in diameter; stamens about 35, the longest filament 6 mm. long; disc and style glabrous, the style slightly shorter than the longest stamens, columnar or slightly divided above; stigma linear, the fertile surface generally abaxial, 1.8 mm. long, the adaxial side when fertile shorter and much narrower than the abaxial. Capsules obovoid, 8–10 mm. long, 7 mm. in diameter, the persistent sepals subapical. Seeds short-tailed, the testa castaneous, reticulate and rugose, the tails half as long as the embryo.

CHINA: Southwest Szechuan: Muli, Wachin, Tin-chang, *T. T. Yu* 14683 (A). Sikang: Tsarung, Upper Salwin River, *J. F. Rock* 22125 (A, NY). Yunnan: Salwin Valley, Sekai, *T. T. Yu* 22992 (A); Kiukiang Valley, *T. T. Yu* 19461 (A), 21003 (A); Wei-se Hsien, *H. T. Tsai* 57954 (A), 59540 (A); Shang-pa Hsien, *H. T. Tsai* 54371 (A), 56524 (A), 58749 (A), 58890 (A), 58927 (A); Che-tze-lo, *H. T. Tsai* 58456 (A); Likiang, *R. C. Ching* 20473 (A), 20718 (A), 20848 (A); same area, *G. Forrest* 2195 (A); *J. F. Rock* 3340 (A), 11445 (A); *C. W. Wang* 71581 (A); Chung-tien, *K. M. Feng* 1420 (A); Haba Snow Range, *K. M. Feng* 1383 (A); Chien-chuan, *J. F. Rock* 8629 (A), 8634 (A, NY); Lan-ping Hsien, *H. T. Tsai* 53740 (A); without precise locality, *H. T. Tsai* 57172 (A); *T. T. Yu* 7085 (A).

TIBET: Latong, *F. Younghusband*, June 29, 1903 (A, G).

UPPER BURMA: Adung Valley, *F. Kingdon Ward* 9461 (A).

CULTIVATED: Europe: Hort. Kew, *C. Schneider*, 1902 (A). United States: Arnold Arboretum no. 6597-2, *A. Rehder*, June 17, 1913 (A) (from Lemoine, with horticultural name recorded by mistake as *Deutzia* 121); Hort. C. S. Sargent, *Veitch-Wilson* 1444, *A. Rehder*, June 12, 1909 (A).

Philadelphus delavayi L. Henry is distinguished by its tomentose leaves, purplish-green pruinose glabrous hypanthium and calyx, columnar style with linear stigmata on the abaxial surfaces, obovoid capsules, and very short-tailed seeds. The tomentum on the lower surface of its leaves resembles that of *P. tomentosus* Wall., its short-tailed seeds resemble those of *P. pekinensis* Rupr., and its linear stigma resembles that of *P. sericanthus* Koehne. Geographically it occurs in an area where the Eastern Asiatic and the Himalayan floras mingle, and morphologically it shows the amalgamation of characters peculiar to species of western Himalaya and central and northern China. It is a well-established species and generally occurs at altitudes 700–3800 meters, in open thickets or by streams in wooded valleys. Its white, fragrant flowers appear in June.

Koehne, in 1906, on the evidence of buds exposed on a winter twig collected in February, decided to place this species in the subsection *Gemmata*. I have observed that the axillary buds of the species of the *Gemmata* are visible on a sterile or flowering shoot during anthesis. Of all the specimens of *P. delavayi* L. Henry that I have examined there is none which has visible axillary buds during the flowering period. Moreover, each of

the buds in the axils of the fallen leaves on the winter twigs is covered by the abscission layer which bursts open as the enclosed bud unfolds. This character is found only in *Euphiladelphus*.

In this species the variation in the size of the leaves and the dentation of the margins is great. In general, the leaves are serrate. *Rock 23815* has uniformly small ovate leaves about 1.5–2 cm. long, with faintly dentate or subentire margins. The large number of branchlets originated from adventitious buds indicates that this specimen was collected from a plant growing under adverse conditions. Variations in the branching or elongation of the pedicels may occur in place of a single flower. For example, *Rock 22125* has cymes on the basal portion of the inflorescences. This tendency to branch, though rare, is not unusual with this species. The photograph published by L. Henry (1903) also illustrates this condition. The pedicels are generally about 1 cm. long. Some fruiting pedicels measure up to 2 cm. long. The calyx in the herbarium specimens of *P. delavayi* L. Henry are all more or less rust-brown in color. Many authors have described the color of the calyx of this species as purplish. But the plant in the Arnold Arboretum has a green calyx.

KEY TO THE VARIETIES

- A. The current year's growth of the stem glabrous.
 - B. Calyx dark purple. a. var. *melanocalyx*.
 - BB. Calyx green tinged with brown. b. var. *cruciflorus*.
 - AA. The current year's growth villose. c. var. *trichocladus*.

32a. *Philadelphus delavayi* var. *melanocalyx* Lemoine ex L. Henry in Rev. Hort. 1903: 14. 1903.—Rehder, Man. Cult. Trees Shrubs 127. 1927.—Chen, Ill. Man. Chin. Trees Shrubs 373. 1937.—Bean, Trees Shrubs ed. 7, 2: 412. 1950.

Philadelphus delavayi sensu Stapf in Bot. Mag. 149: pl. 9022. 1923, non L. Henry.

Philadelphus delavayi f. *melanocalyx* (Lemoine) Rehder, Man. Cult. Trees Shrubs ed. 2, 269. 1940; et Bibl. Cult. Trees Shrubs 192. 1949.

LECTOTYPE: Yunnan, J. F. Rock 4011 (A).

Shrub, the bark of the third year's growth closed, with transverse cracks, tardily wearing off, the second year's growth castaneous, closed, the current year's growth glabrous, striate; leaves ovate-lanceolate, rounded at the base, acuminate at the apex, almost entire, occasionally faintly dentate, uniformly setose above, pubescent on the nerves beneath, 5-nerved; inflorescence 5- up to 9-flowered; hypanthium and calyx glabrous, pruinose, purple; corolla cruciform, 3 cm. across, the petals oblong, 13 mm. long, 9 mm. wide; stamens about 30, the apical third of the style divided.

CHINA: Yunnan: Likiang, J. F. Rock 4011 (A, LECTOTYPE), 4523 (A); R. C. Ching 20848 (A); Chung-tien, K. M. Feng 1420 (A).

The purple calyx variety was first observed by Lemoine de Nancy, who

presented a specimen to Max. Cornu of the Société Nationale d'Horticulture, France. L. Henry published the trinomial but designated no type, hence *Rock 4011* is selected as the lectotype of the variety. Rehder in 1904 treated this taxon as a form. Among the specimens cited above *Rock 4011* and 4523 each has a statement in the field note that the color of the hypanthium and calyx is purplish. These specimens also have ovate-oblong petals which give the corolla a cruciform appearance. The typical *P. delavayi* L. Henry has a green hypanthium and calyx with a brownish tinge, and a discoid corolla with suborbicular petals. The above-mentioned differences are comparable to those that exist between the typical *P. inodorus* Linn. and its varieties. By comparison I think that the varietal rank which L. Henry originally gave to this taxon is better than the status given it by Rehder.

32b. *Philadelphus delavayi* forma *cruciflorus* f. nov.

Frutex, ramulis glaberrimis; foliis ovato-lanceolatis, basi rotundatis vel obtusis, apice acuminatis, serratis vel subintegris; inflorescentiis 7- usque ad 13-floris, floribus solitariis vel cymosis, hypanthiis calycibusque glaberrimis, corolla cruciformi, 4 cm. diametro, petalis oblongis, 2 cm. longis, 8 mm. latis, staminibus ca. 30, disco et stylo glabro, stigmatis linearibus.

CHINA: Yunnan: Wei-si Hsien, C. W. Wang 63781 (TYPE, A).

The indumentum on the leaves of this variety resembles that of *P. delavayi* L. Henry. It can be readily distinguished from the typical form by its cruciform corolla. The corolla of *P. delavayi* L. Henry is disciform.

32c. *Philadelphus delavayi* var. *trichocladus* Hand.-Mazz., Symb. Sin. 7: 438. 1931.

TYPE: *Genestier* 9949 (ISOTYPE, A).

Shrub; bark of the second year's growth castaneous or grayish brown, closed; of the current year's growth crispulo-villose; leaves ovate or ovate-elliptic, acute or rounded at the base, acute or acuminate at the apex, uniformly setose above, the hairs compressed, densely tomentose or velvete beneath, subentire or denticulate; inflorescences 5- up to 12-flowered; hypanthia and calyx glabrous; corolla disciform, 3-4 cm. across, the petals ovate-suborbicular, 1.3-2 cm. long, 9-15 mm. wide.

SOUTHEAST TIBET: (Sikang): *G. Forrest* 19133 (PARATYPE).

CHINA: Yunnan: Tschamutong, *P. Genestier* 9949 (ISOTYPE, A); Atung-tze, Pei-ma-shan, *J. F. Rock* 22755 (A, NY); Tse-chung, *T. T. Yu* 19006 (A); without precise locality, *G. Forrest* 16211 (A), 16412 (A); *T. T. Yu* 6618 (A), 8438 (A).

T. T. Yu 19006 represents an abnormal form. The indumentum on the stems and leaves is extraordinarily thick, the inflorescence tends to be subpaniculate, and some stigmata are bifid.

33. *Philadelphus purpurascens* (Koehne) Rehder in Mitt. Deutsch. Dendr. Ges. 1915(24): 220. 1916.

Philadelphus brachybotrys var. *purpurascens* Koehne in Sargent, Pl. Wils. 1: 6. 1911.

Philadelphus delavayi sensu Hutchin. in Bot. Mag. 136: pl. 8324. 1910, non L. Henry.

Philadelphus nepalensis sensu Diels in Notes Bot. Gard. Edinb. 7: 291. 1912. — sensu Lévl., Cat. Pl. Yunnan 225. 1917, non Koehne.

Philadelphus delavayi var. *calvescens* Rehder in Jour. Arnold Arb. 1: 196. 1919, 5: 236. 1924; Man. Cult. Trees Shrubs 275. 1927; ed. 2, 269. 1940; et Bibl. Cult. Trees Shrubs 192. 1949. — Hand.-Mazz., Symb. Sin. 7: 438. 1931. — Chen, Ill. Man. Chin. Trees Shrubs 372. 1937.

Philadelphus henryi var. *lissocalyx* Hand.-Mazz., Symb. Sin. 7: 438. 1931.

LECTOTYPE: Ta-chien-lu, E. H. Wilson 1346 (A).

Shrub 2–4 m. high; bark of the second year's growth brown, grayish or castaneous, closed, the current year's growth glabrous. Leaves ovate or ovate-lanceolate, those on the sterile branchlets 3.5–8 (rarely up to 11) cm. long, 1.5–4 (rarely up to 6) cm. wide, those on the flowering branch 1.5–6 cm. long, 0.5–3 cm. wide, usually uniformly strigose above, sometimes only the apical half sparsely strigose above, strigose on the nerves beneath, serrate. Inflorescence 5- up to 9-flowered, rarely in weak branches 1- or 3-flowered; hypanthium and calyx glabrous, green tinged with purple, slightly glaucous; sepals ovate, 4–6 mm. long, 3–4 mm. wide; corolla campanulate, 3 rarely up to 4 cm. across, the petals oblong, 1.5–2 cm. long, 9–15 mm. wide; stamens 25 up to 30, the longest 8 mm. long, style and disc glabrous, the style 5 mm. long, the stigmas linear, 1.8 mm. long, abaxial. Capsules obovoid, 7 mm. long, 5 mm. in diameter, the persistent sepals apical. Seeds short-tailed, the tail half as long as the embryo, testa castaneous, reticulate and rugose.

CHINA: S i k a n g (formerly called Western or Southwestern Szechuan): West of Ta-chien-lu (Kanting), E. H. Wilson 1346 (LECTOTYPE, A); Ta-p'ao-shan, NE of Ta-chien-lu, E. H. Wilson 3046 (A); ascending Fu-pien Hsien, F. T. Wang 21368 (A); Muli, mountains of Kulu, J. F. Rock 18024 (A); Mount Kongka, J. F. Rock 16284 (A, NY), 16673 (NY), 16492 (NY); Mt. Siga, J. F. Rock 23815 (A, NY), 24380 (A, NY); between Litang and Yalung Rivers, J. F. Rock 16673 (A); Tsa-wa-rung, C. W. Wang 65583 (A). Y u n n a n : Atungtze, C. W. Wang 69834 (A), 70020 (A); T. T. Yu 10589 (A); northeast of Likiang, Tzai-koo Snow Range, R. C. Ching 21274 (A); west of Likiang, Tamichung, R. C. Ching 21463 (A); west of Likiang, R. C. Ching 21876 (A); northwest of Likiang, I-chi, R. C. Ching 21938 (A); Likiang Snow Range, R. C. Ching 30185 (A), 30294 (A); same region, K. M. Feng 3028 (A); J. F. Rock 4091 (A), 3386 (A), 4522 (A, NY), 3547 (A), 11416 (A), 24846 (A, NY); C. Schneider 1806 (A); 1896 (TYPE of *P. delavayi* var. *calvescens* Rehder, A); C. W. Wang 70650 (A), 70744 (A), 70847 (A), 70973 (A), 71158 (A); T. T. Yu 15066 (A); Haba Snow Range, K. M. Feng 1091 (A); Tali (Dali), Handel-Mazzetti 8696 (ISO-TYPE of *P. henryi* var. *lissocalyx* Hand.-Mazz., A); Tali Range, G. Forrest 5036 (A); west of Tali, J. F. Rock 6813 (A), C. W. Wang 63165 (A); Chung-

tien, *K. M. Feng* 1012 (A), 3300 (A); *T. T. Yu* 13869 (A); Kouty, *Siméon Tén* 469 (A), 543 (A); without precise locality, *H. T. Tsai* 57597 (A); *T. T. Yu* 11316 (A).

CULTIVATED: England: Hort. Veitch, 1768, *E. H. Wilson*, 1911. United States: Arnold Arboretum 6599-1 (Plant Veitch 1768W); 6599-2 = 15413 (Veitch 1778a), *E. H. Wilson*, June 17, 1913 (A); Golden Gate Park, *E. Walther*, May 8, 1932 (A).

This species was first described as *P. brachybotrys* Koehne var. *purpurascens* Koehne on the basis of two specimens collected by E. H. Wilson from western Szechuan (now known as Sikang). No taxonomical type was designated. *Wilson* 1346 has both flower and fruit, and it is here selected as a lectotype.

Philadelphus purpurascens (Koehne) Rehder was introduced into cultivation by E. H. Wilson. The specimens in the Arnold Arboretum indicate that his seed no. 1768W germinated in 1911 in Hort. Veitch and no. 1778a germinated in the same garden in 1913. Number 1768W is associated with Wilson's herbarium specimen no. 1346. In the Arnold Arboretum it is numbered 6599-1.

In 1925 seeds were collected from this plant and germinated by W. H. Judd. *Veitch* 1778a was also introduced in the Arnold Arboretum and is cultivated under the number 15413 = 6599-2. The specimen is rather sick-looking. The calyx is yellowish green with some brownish tinge. It does not appear to be a very ornamental species.

33a. *Philadelphus purpurascens* (Koehne) Rehder var. *venustus* (Koehne), comb. nov.

Philadelphus venustus Koehne in Mitt. Deutsch. Dendr. Ges. 1906: 53. 1906; et in Fedde Repert. Sp. Nov. 6: 335. 1909.

LECTOTYPE: Hort. Vilmorin 3501, *C. Schneider*, June 2, 1906 (A).

Shrub 2-3 m. high; bark of the second year's growth close, gray or brown, the current year's growth uniformly villose; leaves ovate, those on the flowering shoot 1.5-4.5 cm. long, 0.5-2 cm. wide, acute or rounded at the base, acuminate at the apex, uniformly strigose above, the hairs compressed and appressed, strigose on the nerves beneath; inflorescences 5- or 7-flowered; pedicels 3-10 cm. long, glabrous; hypanthium and calyx glabrous; corolla subcampanulate, the petals suborbicular-oblong, 1-1.3 cm. long, 1 cm. wide; disc and style glabrous; stigma linear, 1 mm. long, abaxial.

CHINA: Southwestern Szechuan: Muli, mountains of Kulu, East of Muli Gomba, *J. F. Rock* 16492 (A); between Hunka and Waloho, *C. Schneider* 1529 (A). Yunnan: Sungkwei Range, *G. Forrest* 23069 (A); without precise locality, *T. T. Yu* 6000 (A), 6053 (A).

CULTIVATED: Hort. M. L. de Vilmorin, *Les Barres* 3501, *C. Schneider*, June 2, 1906 (A, probably a specimen from the type plant).

This variety occurs at altitudes of 3650-4425 meters in southwestern Szechuan and adjacent Yunnan.

Koehne described *P. brachybotrys* var. *purpurascens* on the basis of two specimens collected by Wilson. One of these was collected west of Ta-chien-lu and the other from Ta-p'ao-shan, northeast of Ta-chien-lu. According to Koehne *P. venustus* was raised from seeds sent to Vilmorin by a French missionary, Soulié, who was stationed in E. Tibet. We know that Soulié was stationed at Tongolo, a village about twenty-five miles west of Ta-chien-lu. Geographically *P. venustus* Koehne and *P. purpurascens* (Koehne) Rehder are from the same area. Morphologically they differ only in the presence or absence of hair on the current year's growth. *Philadelphus purpurascens* (Koehne) Rehder is a better known taxon in the botanical literature, and as represented by the Arnold Arboretum collections, it also has a wider range than Koehne's *P. venustus*, which I consider a pubescent variety.

Series 6. **Pubescentes**, ser. nov.

Philadelphus subg. II. **Euphiladelphus** sect. 4. **Stenostigma** ser. 6.
Pubescentes, ser. nov.

Philadelphus sect. *Stenostigma* subsect. *Gordoniani* Koehne in *Gartenfl.* 45: 450, 542. 1896; et in *Mitt. Deutsch. Dendr. Ges.* 1904 (13): 81. 1904, pro parte.

Philadelphus Coronarii Rydb. in *N. Am. Fl.* 22: 162. 1905, in clavi, s. stat.

Philadelphus ser. *Gordoniani* (Koehne) Rehder, *Man. Cult. Trees Shrubs* ed. 2, 207. 1940; et *Bibl. Cult. Trees Shrubs* 191. 1949, pro parte.

TYPE SPECIES: *P. pubescens* Loisel.

Frutices grandes, ramulis cinereis, bienniis cortice clauso, hornotinis glabris; foliis ovatis vel ovato-ellipticis, supra praeter nervos primarios glabris, subtus dense strigoso-villosis; inflorescentiis 7-, 9-, raro 5- vel 11-floris; hypanthiis calycibusque pubescentibus; capsulis obovoideis; seminibus medie caudatis.

The center of distribution of the species of this series, as shown in map 3, is the Nashville Basin. The range extends northward to Pope County in Illinois and southwestward to the Ozark Plateau and the Ouachita Mountains. Species of this series are characterized by very pubescent leaves, hypanthia and calyces, and by medium-caudate, relatively large seeds. These characters suggest that the closest relationship is with the Chinese series *Sericanthi*, especially the species that occur in the peneplains of northwestern Hupei, eastern Szechuan and Kweichow.

KEY TO THE SPECIES

A. Style and disk glabrous; base of the corolla glabrous. 34. *P. pubescens*.
 AA. Style and disk pubescent; base of the corolla pubescent on the outside. 35. *P. gattingeri*.

34. *Philadelphus pubescens* Loiseleur, *Herb. Gén. Amat.* 4: *pl. 268.* 1820. — Drapiez, *Herb. Amat. Fl.* 6: *pl. 440.* 1833. — Koehne in

Gartenfl. 45: 542. 1896; et in *Mitt. Deutsch. Dendr. Ges.* 1904(13): 81. 1904. — *Schneider, Dendr. Winterst.* 186. 1903; et *Ill. Handb. Laubh.* 1: 369, *fig. 235, f-m.* 1905. — *Apgar, Orn. Shrubs U. S.* 197, *fig. 310.* 1910. — *Moore in Bailey, Stand. Cycl. Hort.* 5: 2581. 1916. — *Trelease, Wint. Bot.* 74. 1918. — *Starcs, [Handb. Trees Shrubs Latvia]* 158. 1925. — *Rehder, Man. Cult. Trees Shrubs* 273. 1927; ed. 2, 267. 1940; et *Bibl. Cult. Trees Shrubs* 191. 1949. — *Bean, Trees Shrubs* ed. 7, 2: 418. 1950. — *Fernald, Gray's Man. ed. 8,* 747. 1950. — *Gleason, Ill. Fl.* 2: 273. 1952.

Philadelphus grandiflorus sensu Ker in *Bot. Reg.* 7: *pl. 570.* 1821. — sensu P. W. Watson, *Dendr. Brit.* 1: *pl. 46.* 1824. — sensu Walp., *Repert.* 2: 151. 1843, *pro parte, non Willd.*

Philadelphus latifolius Schrader ex DC., *Prodr.* 3: 206. 1828; et in *Linnaea* 12: 394. 1838. — *Louden, Arb. Frut. Brit.* 2: 953, *fig. 676.* 1838. — *Schneider, Ill. Handb. Laubh.* 1: 369, *fig. 237, i-l.* 1905. — *Rydb. in N. Am. Fl.* 22: 168. 1905. — *Syereihtchikof (Suiereishchikow), Ill. Fl. Mosc.* 2: 221, *fig. [2].* 1907. — *Beadle in Small, Fl.* 507. 1903; ed. 2, 507. 1913; et in *Small, Man. South. Fl.* 599. 1953. — *Starcs, [Handb. Trees Shrubs Latvia]* 159. 1925.

Philadelphus discolor Rafin., *Autikon Bot.* 149. 1840. — *Merr., Ind. Rafin.* 135. 1949.

Philadelphus grandiflorus var. *floribunda* Gray, *Fl. N. Am.* 1: 595. 1840.

Philadelphus latifolius var. *pubescens* Dippel, *Handb. Laubh.* 3: 339. 1893.

Philadelphus dubius hort. ex Koch, *Dendr.* 1: 343. 1896.

TYPE: *M. Fraser.*

A stiff, tall shrub up to 5 m. high, the branches cinereous, the second year's growth 3–4 mm. across, the bark closed, with few transverse cracks. the current year's growth glabrous. Leaves ovate or broad-ovate, those on the vegetative shoots 4–8 (rarely to 15) cm. long, 3.5–6.5 (rarely to 10.5) cm. wide, those on the flowering shoots 4–8 cm. long, 3–5.5 cm. wide, rounded at the base, abruptly short-acuminate at the apex, the acumen 3–10 (rarely to 20) mm. long, remotely denticulate or subentire, glabrous with the principal nerves sparsely scabrid-pilose above, uniformly strigose-villose beneath. Inflorescences 7-, 9-, rarely 5- or 11-flowered, the lower pairs in the axils of normal leaves; pedicels, hypanthium and sepals uniformly strigose-villose, the sepals ovate, 6–7 mm. long, the apex acuminate; corolla cruciform, 3.5 cm. across, the petals obovate-oblong, 12–15 mm. long, 10–12 mm. wide; stamens ca. 37, the longest 9 mm. long; disc and style glabrous, the stigmata oar-shaped, the adaxial and abaxial stigmatic surfaces about the same length. Capsules obconic, 7–9 mm. long, 5 mm. in diameter, the persistent calyx subapical. Seeds rather large, the embryos ellipsoid, 2 mm. long, 0.75 mm. in diameter, the tail 1.5 mm. long. the lobes of the crown pointed.

UNITED STATES: Illinois: Pope Co., Golconda, *E. J. Palmer* 19581 (A, F, G, MO), 22582 (A, F, MO). Tennessee: Cheatham Co., Kingston Spring, *H. Eggert*, Aug. 19, 1897 (MO, NY); Davison Co., Nashville, *T. G. Harbison* 63

(A), *E. B. Harger* 7808 (G, TENN); *A. Gattinger* 838 (F 205899C, F 309472A); Montgomery Co., Clarksville, *E. J. Palmer* 17625 (A, F), 17629 (MO). Arkansas: Faulkner Co., Hardinville, *E. J. Palmer* 26539 (A); Garland Co., Gulpha Creek, *E. J. Palmer* 24950 (A); Logan Co., Magazine Mountain, *E. J. Palmer* 23228 (A, G, MO, US); Newton Co., Jasper, *E. J. Palmer* 6934 (A, F, US), 27087 (A, MO); Van Buren Co., *G. M. Brown*, June 9, 1909 (A), May 8, 1910 (A). Oklahoma: Le Flore Co., Rich Mountain, *E. J. Palmer* 20623 (A, US); *F. A. Merk*, Oct. 20, 1935 (MO).

CULTIVATED: Europe: Kew, *Macklearn* 453 (BH), *G. Nicholson* 1609 (A); Hort. Vilmorin, 1928 (A); Hort. Plantières, *C. Schneider*, Sept. 13, 1903 (A), June 25, 26, 1906 (A); Hort. Bot. Berol., *E. Koehne* 11 (MO); Breslau, Gopperthain, *C. Baenitz*, June 16, 1905 (BH, US), July 1, 1902 (F), June 11, 1907 (BH, US); Hort. Götting, *A. Rehder* 396 (A), 1662 (A), 1637 (A, MO); Bot. Gart. Forstakademie Hannover 56, *H. Zabel* (A); Hort. Bot. Petropolitano (A); Hort. Bot. Leipzig, *C. K. Schneider*, June 25, 1904 (A); Hort. Späth, *C. K. Schneider* in 1902 (A); Les Barres, *C. Schneider*, June 6, 1906 (A). Canada: Ottawa, Central Exper. Farm, *R. A. Inglis*, July 6, 1916 (BH); Dominion Arboretum X-2-148, *J. M. Gillett* 185 (BH). United States: Arnold Arboretum 543-3, *G. M. M.*, June 22, 1923 (BH), 1059-36, *R. B. Clark*, June 13, 1941 (BH), 2221, without collector, June 28, 1888 (A); 226-1, *W. H. Manning* in 1892 (BH), 6840, without collector, June 30, 1913 (A), Sept. 10, 1913 (A), 2213-1, without collector, June 20, 1904 (A), June 27, 1904 (A); Ithaca, Herb. Bailey, June 25, 1925 (BH), Sept. 10, 1928 (BH); Highland Park, Rochester, *R. E. Horsey*, Sept. 4, 1918 (BH); Kansas State Agr. College, *E. A. Papenoe*, June 7, 1901 (US); St. Louis, *E. E. Sherff*, July 13, 1910 (F); Garden of Anson & Anita Blake, Cal., *N. F. Bracelin* 2728 (BH); Pine, Indiana, *C. W. Duesner*, 1908 (F). Australia: Roy. Hort. Soc. Garden, Wisley, Surrey, June 1933 (BH).

Philadelphus pubescens was validated by the publication of a colored plate and a careful description of a five-year-old plant cultivated in the garden of M. Noisette, who got it from Fraser, a British botanical explorer. G. M. Brown's collection from Arkansas matches Loiseleur's illustration the best, and the identification of the specimens cited above is done by comparing them with that collection.

Schrader in 1828 and 1838 characterized *P. latifolius* Schrader as a plant with broad-ovate, long-acuminate leaves. He recognized *P. latifolius* hort. and *P. pubescens* hort. as conspecific and stated that the plant was a native of North America. He overlooked Loiseleur's earlier valid publication of the specific name and chose *P. latifolius* instead of *P. pubescens*. Thus his choice becomes a synonym of the latter binomial.

According to Rafinesque's description, *P. discolor* has glabrous branchlets, broad-ovate or subcordate leaves glabrous above, white-pilose beneath, and terminal subracemose flowers. This is a very good description of *P. pubescens* Loisel.

Philadelphus pubescens Loisel. is the most commonly cultivated species. Many names have been used in the trade or gardens. Among the specimens received by the Arnold Arboretum are plants named *P. cordifolius* (Vilmorin), *P. gordoniianus* (Kansas, Späth), *P. grandiflorus* (Kew), *P. globosus* (Plantières), *P. inodorus* var. *grandiflorus* (Kew), *P. incanus* (Can-

ada), *P. nivalis* (Plantières), *P. insignis* (Les Barres), *P. verrucosus* (many), *P. zeyheri* (Germany), and several other unpublished binomials. The lack of discrimination in naming the species in botanical gardens may have been the cause of some undue statements in the conclusions of cytologists.

34a. ***Philadelphus pubescens* var. *verrucosus* (Schrader), comb. nov.**

Philadelphus verrucosus Schrader ex DC., Prodr. 3: 205. 1828; et in Linnaea 12: 40. 1838.—Loudon, Arb. Frut. 3: 952, fig. 675. 1838.—Lavallée, Arb. Segrez. Enum. 115. 1877.—Rehder in Jour. Arnold Arb. 2: 154. 1921; Man. Cult. Trees Shrubs 273. 1927; ed. 2, 267. 1940; et Bibl. Cult. Trees Shrubs 191. 1949.

Philadelphus rhombifolius Rehder in Jour. Arnold Arb. 1: 195. 1920.—Nemato, Nippon Shok. Sor. Hoi 294 (Fl. Jap. Suppl.). 1936.

TYPE: Conservatoire et Jardin botaniques, Genève, Schrader 1827.

A tall erect shrub, the branches gray, the current year's growth glabrous; leaves elliptic, ovate-elliptic or oblong-elliptic, those on the vegetative shoot 6.5–15 cm. long, 4–9 cm. wide, those on the flowering shoot 3.5–10 cm. long, 1.5–5 cm. wide, acute or obtuse at the base, abruptly short-acuminate at the apex, subentire or remotely serrate or dentate, glabrous above, uniformly strigose-villoso beneath, inflorescences 7-, 9-, or 5-flowered.

UNITED STATES: Illinois: Pope Co., Golconda, *E. J. Palmer* 15438 (A, MO), 23021 (A), 23773 (A, MO). Missouri: McDonald Co., Southwest City, *J. A. Steyermark* 5573 (F, MO), 65196 (F). Tennessee: Cheatham Co., Pegram, *H. K. Svenson* 10297 (G, MO, TENN); Biltmore Herb. 5836 (A, G, MO, NY, US), 5836a (G); *E. P. Bicknell*, May 14, 1894 (NY); *L. G. Charlesworth* 3717 (TENN); *A. Gattinger* 838 (G, MO, NY, TENN); Montgomery Co., *A. & E. Clebsch*, May 18, 1946 (TENN). Arkansas: Independence Co., Batesville, *D. Demaree* 17058A (NY); Hempstead Co., *J. M. Greenman* 4416 (MO); *E. J. Palmer* 24028 (A, US), 24997 (A); Garland Co., *E. J. Palmer* 29155 (A); Hot Spring Co., *E. J. Palmer* 29713 (A); Logan Co., *E. J. Palmer* 24153 (A); Van Buren Co., *G. M. Brown*, May 8, 1910 (A). Oklahoma: Le Flore Co., Rich Mountain, *E. J. Palmer* 22249 (A).

CULTIVATED: Europe: Kew, *G. Nicholson* 1583 (A); Bot. Gart. Forstakademie Hannover, 4, *H. Zabel*, June 30, 1873 (A), Sept. 1, 1873 (A). Asia: Japan: Prov. Musasi, without collector, June 30, 1910 (TYPE of *P. rhombifolius* Rehder). Canada: Ottawa, Dominion Arboretum X-2-150, *J. M. Gillett* 179 (BH), X-2-172, *J. M. Gillett*, July 3, 1939 (BH); 96-147-38, *J. M. Gillett*, July 3, 1939 (BH). United States: Arnold Arboretum 542-1, *W. H. Manning* in 1892 (BH), 2214-1 = 15375, *A. Rehder*, July 18, 1918 (A), June 19, 1919 (A), July 9, 1920 (A); 2214-3 = 15376, *A. Rehder*, June 20, 1920 (A); Ithaca, Herb. Bailey, June 28, 1916 (BH); Cherokee Park, Louisville, *M. Slack*, 1939 (BH); Missouri Bot. Gard., *H. Kellogg*, May 1902 (US).

Most modern authors interpret *P. verrucosus* Schrader as a synonym of *P. pubescens* Loisel. Rehder re-established Schrader's species on the basis of Palmer's discovery on the rocky bluffs of the Ohio River in Golconda, Illinois. He claimed that the stem of this species is exfoliate. Palmer col-

lected several numbers in that locality. None of the second year's growth has exfoliate bark. *Palmer* 15438 has some third year's growth of which the bark has partially worn off.

When Schrader published *P. verrucosus* he compared it with *P. pubescens* Loisel. (= *P. latifolius* Schrader). He distinguished them by their leaf forms. Schrader's type is very fragmentary. His plate clearly depicts a plant with elliptic or ovate-elliptic leaves acute or obtuse at the base. In the spontaneous flora of southeastern United States this form exists side by side with the typical *P. pubescens* Loisel., which has ovate leaves rounded at the base. The nature and density of the indumentum of this elliptic-leaved form resembles that of *P. pubescens*. I think it deserves no higher rank than that of variety.

The type of *P. rhombifolius* Rehder is not a Japanese *Philadelphus*. A plant with long strigose-villoso pubescent hypanthia, sepals, and leaves is not known in the spontaneous Japanese flora. It matches *P. pubescens* Loisel. very well and must have come from cultivated material.

35. *Philadelphus gattingeri*, sp. nov.

Frutex grandis, ramis cinereis, bienniis 3 mm. diametro, cortice clauso, hornotinis glabris, nodis eciliatis; foliis ovatis vel ovato-oblongis, 3-6.5 cm. longis, 1.5-3.2 cm. latis, basi rotundatis, raro obtusis, apice acutis, raro breviter acuminatis, integris, raro utrinque 1 vel 2 dentibus inconspicuis, supra glabris, ad nervos strigoso-pilosus, subtus uniforme strigoso-villosus, pilis incanis, basi curvatis; inflorescentiis 9- raro 5-floribus, paribus inferioribus in axillis foliorum positis; pedicellis, hypanthiis et calycibus strigoso-villosis, pilis incanis, sepalis ovatis 5 mm. longis, 3-4 mm. latis, apice acutis; corolla disciformi, 3 cm. diametro, petalis obovatis, 1.3 cm. longis, 1.2 mm. latis, apice rotundatis, basi dorsis pilosis; staminibus ca. 35; disco et stylo pilosis, stigmatibus spatulatis.

UNITED STATES: Tennessee: Bluffs of Cumberland River near Nashville, *A. Gattinger* 838 (US 1119570, TYPE; F 205899B, F 309472B, MO 775002, NY, US 25563, US 772375, ISOTYPES).

Gattinger 838 involves three different elements, *P. hirsutus* Nutt., *P. pubescens* Loisel., and the type material of *P. gattingeri*. In order to distinguish this material from specimens pertaining to the other two species, the accession numbers of the herbaria where the type and isotypes are deposited are also given. This species is closely related to *P. pubescens* Loisel., from which it can be distinguished readily by its pubescent style.

Series 7. *Sericanthi* Rehder

Philadelphus subg. II. *Euphiladelphus* sect. 4. *Stenostigma* ser. 7.

Sericanthi Rehder in Jour. Arnold Arb. 1: 196. 1920; Man. Cult. Trees Shrubs ed. 2, 269. 1940; et Bibl. Cult. Trees Shrubs 192. 1949.

Philadelphus sect. *Stenostigma* subsect. *Satsumani* Koehne in Gartenfl. 45:

450, 561. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 82, 84. 1904.
pro parte.

TYPE SPECIES: *P. sericanthus* Koehne.

Shrubs of medium height, the branches gray, the second year's growth brown, castaneous or gray, the bark moderately exfoliate or closed and slowly wearing off; leaves ovate or ovate-elliptic, pubescent, at least on the primary nerves beneath; inflorescence racemose, rarely paniculate, 7-, 9-, rarely 15- or 3-flowered; hypanthia more or less pubescent; capsules obovoid or obconic; seed short- or medium-caudate.

This series contains a heterogeneous group of the Chinese species of *Philadelphus* which have more or less pubescent hypanthia. The density and the type of the hairs on the hypanthia vary considerably. In some species, such as *P. incanus* and *P. reevesianus*, the epidermal tissue of the hypanthium is completely obscured by the white strigose hairs, and in other species, as *P. tenuifolius*, the epidermal tissue of the hypanthium is largely exposed and the hairs are very sparse, often only present at the basal portion of the hypanthium. Phytogeographically, species of this series are concentrated on the Tsinling Range, from the western end of which the distribution extends in accordance with the north-south Sino-Tibetan Mountains southward to Yunnan and northward to Kansu. From the eastern end of the Tsinling Range the distribution extends southward, reaching the Kweichow Plateau and the northern section of Kiangsi. It is interesting to point out that the species that occur in this eastern area are morphologically very similar to species of the Ozark Plateau. The species that occur in the southeastern highlands of Manchuria are comparatively more remotely related to the West China members of this series. The distribution of the species of this series is shown in maps 5 and 7.

KEY TO THE SPECIES

- A. Hypanthia densely covered by white hair, the tissue beneath obscured.
- B. Style and disc glabrous.
 - C. Hairs on the hypanthia strigose, appressed; leaves pubescent.
 - D. Anthers glabrous 36. *P. incanus*.
 - DD. Anthers setose 37. *P. reevesianus*.
 - CC. Hairs on the hypanthia villose and erect; leaves glabrous (except some cultivated forms). 38. *P. dasycalyx*.
- BB. Rim of disc setose; hair on the hypanthia long-villose, erect. 39. *P. mitsai*.
- AA. Hypanthia sparsely covered, the tissue beneath visible.
 - B. Disc and style glabrous.
 - C. Hypanthia and sepals uniformly covered.
 - D. Leaves on the flowering branches serrate; hairs on the hypanthia strigose. 40. *P. sericanthus*.
 - DD. Leaves on the flowering branches entire or faintly denticulate; hair on the hypanthia scabrid. 41. *P. henryi*.
 - CC. Hypanthia partially covered, the hairs usually occurring at the base. sepals usually glabrous. 42. *P. tenuifolius*.
 - BB. Disc, style, or both pubescent.

C. Hair on the hypanthia golden and crisp, appressed, or villose-sublanate.
 D. Leaves uniformly pubescent beneath; style and disc crisp villose. 43. *P. subcanus*.
 DD. Leaves almost glabrous, strigose only on the primary nerves beneath; style glabrous, rim of disc setose. 44. *P. kansuensis*.
 CC. Hair on the hypanthia straight, pilose, or strigose.
 D. Leaves ovate, rarely ovate-elliptic, subentire or denticulate; style half or more divided, the stigmata clavate; hypanthia pilose, the sepals glabrous. 45. *P. schrenkii*.
 DD. Leaves elliptic, prominently sharp-serrate; style undivided, the stigmata spatulate; hypanthia strigose, the hair incanous. 46. *P. hupehensis*.
 36. ***Philadelphus incanus* Koehne in Gartenfl. 45: 562. 1896, exclud. specim. Henry 8823; in Mitt. Deutsch. Dendr. Ges. 1904(13): 84. 1904; in Sargent, Pl. Wils. 1: 5. 1911 et 1: 145. 1912. — Schneider, Ill. Handb. Laubh. 1: 370. 1905. — Diels in Bot. Jahrb. 29: 371. 1900. — Smith in Jour. Linn. Soc. Bot. 36: 500. 1905. — Wilson, Arnold Arb. Exp. China 1910–11, pl. 27. 1912. — Bean, Trees Shrubs 2: 135. 1914; ed. 7, 2: 414. 1950; et in Chitt., Dict. Gard. 3: 1546. 1951. — Hers in Jour. N. China Branch Roy. As. Soc. 53: 113. 1922; et List. Ess. Lign. Honan. 20. 1922. — Rehder in Jour. Arnold Arb. 5: 153. 1924; Man. Cult. Trees Shrubs 274. 1927; ed. 2, 268. 1940; et Bibl. Cult. Trees Shrubs 192. 1949. — Chen, Ill. Man. Chin. Trees Shrubs 371, fig. 278. 1937.**

Philadelphus coronarius var. *tomentosus* sensu Forbes & Hemsl. in Jour. Linn. Soc. Bot. 23: 277 (Ind. Fl. Sin. I). 1887, non Hook. f. & Thoms.

LECTOTYPE: *A. Henry* 6093 (A).

A stiff erect shrub 1.5–3.5 m. high; the second year's growth gray, closed, or brown, tardily exfoliating; current year's growth villose. Leaves ovate, elliptic, or rarely elliptic-lanceolate, 4–8.5 cm. long, (1–) 2–4 cm. wide, those of the vegetative shoots up to 10 cm. long, 6 cm. wide, sparsely setose above, the hairs erect, uniformly strigose-villose beneath, the hairs appressed, serrate. Inflorescence 7- or 11-flowered, the lower pairs usually in the axils of normal leaves; the rachis pubescent; pedicels 5–10 mm. long, incanous, the hypanthium and calyx densely covered with appressed white hair, the underlying tissue not visible; sepals ovate, 4–5 mm. long, 3–3.5 mm. wide, the apex acute or acuminate; corolla subcampanulate disciform, 2.5–3 cm. across, the petals obovate or suborbicular, 1.3–1.5 cm. long, 0.8–1.3 cm. wide, sparsely strigose at the base of the back; stamens ca. 34, the longest 10 mm. long; disc and style glabrous, the style 5 mm. long, slightly divided at the apex, the stigmata clavate, the abaxial surface 1.8 mm. long, the adaxial slightly longer. Capsules obovoid, 7–9 mm. long, 4–7 mm. in diameter, the persistent sepals super-median. Seeds very short-caudate, the embryo 1.5 mm. long, the tail half as long.

CHINA: Shensi: Kan-y-san, *Jos. Giraldi*, June 11–12, 1897 (A); Lao-y-

san, *Jos. Giraldi*, Sept. 6, 1897 (A). Western Hupei: Ichang and vicinity, Gian-gia-kwan, *W. Y. Chun* 3555 (A), 3819 (A); Siu-yeh-sie, *W. Y. Chun* 3706 (A) = Herb. Nanking no. 4084 (A); Tan-shu-ya, *W. Y. Chun* 3758 (A), Wang-sung-gon, *W. Y. Chun* 3782 (A); Suon-nai-vok, *W. Y. Chun* 4181 (A); same area, *A. Henry* 3625 (G, NY), 3949 (A, ISOSYNTYPE, G), 6093 (A, LECTOTYPE); *E. H. Wilson* 583 (A, G), 3049 (A); Nan-to, *A. Henry* 2143 (G); Fang Hsien, *E. H. Wilson* 3047 (A); Hsing-shan-Hsien, *E. H. Wilson* 574 (A, G), 3048 (A), 3054 (A), 3055 (A); Chang-lo Hsien, *E. H. Wilson* 3051 (A), 3052 (A); Pa-tung Hsien, *H. C. Chow* 262 (A, NY), 544 (A, NY), 796 (A), same area, *E. H. Wilson* 3053 (A); without precise locality, *C. Silvestri* 4370 (A); *A. N. Steward* ex Herb. Univ. Nanking no. 9775 (A); *E. H. Wilson* 833 (NY), June 1907 (A).

CULTIVATED: Europe: Hort. Vilmorin (*Wilson* 583) (A); Les Barres, *L. Pandé*, in 1922 (A). Australia: Roy. Hort. Soc. Garden, Wisley (A). United States: Arnold Arboretum 15368 = 6529-3 (*Wilson* 574), without collector, Oct. 7, 1912 (A); *A. Rehder*, July 18, 1918 (A); Arnold Arboretum 7338 (*Wilson* 581), without collector, July 9, 1915 (A), *A. Rehder*, June 24, 1919 (A); Arnold Arboretum 15369 = 6529-4 (*Wilson* 583), without collector, July 9, 1915 (A), Oct. 7, 1912 (A); Highland Park, Rochester, *E. H. Costich*, July 3, 1916 (A); Pa. State College, *R. P. Meahl*, June 1937 (A).

In 1911 *E. H. Wilson* collected three lots of seeds of this species and numbered them 574, 581, and 583. They all germinated in 1912. Plants from lot 574 flowered in 1918, while those from lots 581 and 583 flowered in 1915. The Vilmorin Nursery also obtained some seed of Wilson's Lot 583. The United States Department of Agriculture bought some plants from Vilmorin and assigned a number *S. P. I.* 73280. The plant in the Botanical Garden of Pennsylvania State College is from that source.

Forbes & Hemsley interpreted Henry's collection from Nanto, Hupei, as *P. coronarius* Linn. var. *tomentosus* Hook. f. & Thoms. The material that Hooker and Thomson wrote about was from the western Himalayan region. It is altogether different from the species of Central China.

The seeds of this species strongly resemble those of *P. pekinensis* Rupr. The embryo is large and fat with a very short square tail and a crown of rounded lobes. In the density of the indumentum of the leaves *Chow* 262 and 544 appear intermediate between *P. incanus* Koehne and *P. sericanthus* Koehne. The upper surface of the leaves of these two specimens is glabrous and the lower surface is pubescent only on the principal nerves and veinlets. They are placed under *P. incanus* on account of their incanous hypanthia.

Steward's collection is distributed under two sets of labels with the same number. The title of one collection is the Flora of Hupeh. It has field data in typewritten form. The title of the other collection is Flora of Honan. It has no field data. For the sublocality it is stamped "Ki-kung-shan," and the date of collection is Aug. 3, 1925. These specimens are identical in all respects. There is confusion in the labels. The one labeled Flora of Hupeh is the correct label.

Judged by the above-cited specimens, this species appears to be geographically isolated and morphologically stable. It is endemic to the eastern end of the Tsinling Range at the confluence of the Han-hsiu and

Yangtze tributaries, on the border of Shensi, Honan and Hupei provinces. There it grows in woods, on cliffs or by the side of streams at altitudes of 600 to 2300 meters. Its white flowers appear in July. With the exception of *Chow* 262 and 544 little variation exists.

36a. *Philadelphus incanus* var. *Baileyi* Rehder in *Gent. Herb.* 1: 27. 1920; et in *Jour. Arnold Arb.* 5: 153. 1924.

TYPE: *L. H. Bailey*, June 13, 1917 (A).

A low shrub, the branchlets gray, with close and longitudinally rimulose bark, the current year's growth densely strigose, the hairs appressed; leaves ovate, 3-4.5 cm. long, 1.2-2.4 cm. wide, obtuse at the base, acuminate at the apex, the acumen up to 8 mm. long, glabrous above, uniformly strigose beneath, serrate; inflorescences 5- or 7-flowered, the flowers crowded, the rachis 1-2.5 cm. long; pedicels very short, 1-2 mm. long, with the hypanthium and calyx densely strigose, the hairs short, appressed; sepals broad ovate, 4.5 mm. long, 2.5 mm. wide, the apex acute; corolla 2.5 cm. across, the petals obovate, 2.2 cm. long, 0.7 cm. wide, the back glabrous, occasionally with a few crisp weak hairs; stamens ca. 34, the longest 6 mm. long, the anthers subglobose, largely sterile, disc and style glabrous, the style short, 3.5 mm. long, the stigmata subspatulate, appearing sterile; capsules not known.

CHINA: Honan: Chi-kung Shan, border of Hupei and Honan, on the divide between the Yangtze and Hwai-ho, *L. H. Bailey*, June 13, 1917 (A, TYPE; BH), June 16, 1917 (BH).

In the nature of the indumentum this variety resembles *P. incanus* Koehne. In the crowded inflorescences it resembles *P. brachybotrys* Rehder. Its range of distribution is intermediate between that of those two species. The sterility of the anther and stigmata seems to suggest the possibility of it being a natural hybrid of those species. The presence of the adventitious branches and the partially dried, short lateral twigs indicates that the plant was an old one lacking vigor in growth.

37. *Philadelphus reevesianus*, sp. nov.

Philadelphus incanus sensu Koehne in Sargent, *Pl. Wils.* 1: 5. 1911, pro parte.

Frutex 3-4 m. altus, ramulis cinereis vel griseo-cinereis, bienniis longitudinaliter rimulosis, hornotinis scabro-villosis; foliis ellipticis vel ovato-ellipticis, 4-9 cm. longis, 2-5 cm. latis, basi obtusis vel rotundatis, apice acuminatis, acuminibus 5-15 mm. longis, utrinque strigosis, pilis supra erectis, subtus adpressis, margine serratis; inflorescentiis 7- vel 9-floris, rhachibus 2-6 cm. longis, strigoso-villosis; pedicellis 4-5 mm. longis, pilis strigosis, incanis; hypanthiis calycibusque incanis; sepalis ovatis, 6 mm. longis, 3-3.5 mm. latis, apice acuminatis; corolla subcruciformi, 3.5 cm. diametro, petalis oblongis, 1.6 cm. longis, 1 cm. latis, basi dorso strigoso; staminibus ca. 40, antheris oblongis, thecis setosis; discis pubescentibus;

stylis glabris vel basi hirtellis, 5 mm. longis, apice liberis; stigmatibus spathulatis; capsulis subglobosis, 7 mm. diametro, sepalis persistentibus subapicalibus; seminibus breviter caudatis, 2-3 mm. longis, testis fuscis.

CHINA: H u p e i : Chang-yang Hsien, *E. H. Wilson* 3050 (TYPE, A).

CULTIVATED: Arnold Arboretum 15367 (Veitch trip, *Wilson* 915), flowered July 10, 1912.

The type specimen of this species was collected in central China by Wilson in 1907. Due to its superficial resemblance to *P. incanus* Koehne, it has been erroneously interpreted as that species. Koehne's species has glabrous anthers and disks, while both the spontaneous material of Wilson's collections and the cultivated plant in the Arnold Arboretum have distinctively setose anthers and pubescent disks. In fact, this is the only Old World form with setose anthers, and I consider this character sufficient to give it specific status.

This species is named in memory of my first botany teacher, Dr. Cora D. Reeves, Founder and Head of the Department of Biology, Ginling College, Nanking, China. Her twenty-five years of unselfish service in the field of Chinese Biology have established a permanent monument among Chinese botanists as well as zoologists of my generation.

38. *Philadelphus dasycalyx* (Rehder), stat. nov.

Philadelphus pekinensis var. *dasycalyx* Rehder in Jour. Arnold Arb. 1: 197. 1920.—Hers in Jour. N. China Branch Roy. As. Soc. 53: 113. 1922; et List. Ess. Lign. Pl. Honan 20. 1922.—Chen, Ill. Man. Chin. Trees Shrubs 373. 1937.

TYPE: N. Honan, Hwei Hsien, *J. Hers* 713 (A).

A subscandent shrub, the bark of the second year's growth castaneous, exfoliating; the current year's growth glabrous or glabrescent. Leaves ovate or ovate-elliptic, 3-6 cm. long, 1.2-3.4 cm. wide, obtuse or rounded at the base, acute or shortly acuminate at the apex, subentire, faintly denticulate or serrate, those on the flowering shoot glabrous on both surfaces, except occasionally with a few hairs on the primary nerves beneath. Inflorescence 5- or 7-flowered, the rachis 1.5-4.5 cm. long, villose; pedicels 5-6 mm. long, villose; hypanthium and calyx sparsely villose, the hairs more or less erect; sepals ovate, 5-6 mm. long, 3 mm. wide, the apex acuminate; corolla subdisciform, 2.5 cm. across, the petals obovate, 1.3 cm. long, 1 cm. wide, glabrous, stamens ca. 34, the longest 7 mm. long; disc and style glabrous, the style and stigmata together 6 mm. long, the stigmata clavate, the abaxial surface short, 0.75 mm. long, the adaxial ones twice as long. Capsules obovoid, 6 mm. long, 4.5 mm. in diameter, the persistent sepals subapical. Seed very short-tailed, the testa brown, the embryo 1.8-2 mm. long, the tail one third as long.

CHINA: Honan: Hwei Hsien, on the Shansi border, *J. Hers* 713 (TYPE, A). Shansi: Nan-yang Shan, *J. Hers* 2729 (A); Chieh-hsiu Hsien, Cho-mei

Shan, *H. Smith* 569 (A); Yüan-chü Hsien, Shai-wang-p'ing, *H. Smith* 6738 (A); Lu-yah Shan, *H. Smith* 8190 (A); Lin-shih Hsien, *T. Tang* 865 (A).

CULTIVATED: Highland Park Nursery no. 15, seed from J. Hers, *R. E. Horsey*, June 24, 1926 (A); Arnold Arboretum no. 20442, *E. J. Palmer*, June 5, 1936 (A).

This species occurs in western Honan and southern, central, and western Shansi. It grows on slopes of wooded ravines at altitudes of 1300–2500 meters. Its white flowers usually appear in late May and early June. *Smith* 8190 was collected in flower in mid-July. All the spontaneous material cited above has glabrous leaves. The vernacular name reported is *Ya-kin-tze*.

Rehder interpreted this taxon as a variety of *P. pekinensis* Rupr. Its short-caudate seeds, crowded inflorescences and small, ovate acuminate leaves resemble those of *P. pekinensis*, but its pubescent hypanthium suggest a closer relationship with the pubescent species of the Sericandi than with the glabrous plants of the Pekinense.

39. *Philadelphus mitsai*, sp. nov.

Philadelphus subcanus sensu Hers in *Jour. N. China Branch Roy. As. Soc.* 53: 113. 1923; et *List. Ess. Lign. Honan* 20. 1922, non Koehne.

Philadelphus incanus sensu Rehder in *Jour. Arnold Arb.* 5: 153. 1924.—sensu Liu in *Bull. Peking Soc. Nat. Hist.* 2 (3): 103. 1928, non Koehne.

Frutex humilis, ramulis cinereis, hornotinis criso-villosis; foliis ovatis, 3–4.5 mm. longis, 1–2.5 cm. latis, basi obtusis, apice acuminatis, acumine 7–10 mm. longo, crasse serratis, supra hispidulis, pilis erectis, subtus sparse villosis; inflorescentiis 7- vel 9-floribus, rhachibus villosis, 2–5 cm. longis, pedicellis 5–6 mm. longis, dense villosis; hypanthiis calycibusque villosis, sepalis ovatis, 6 mm. longis, 3 mm. latis, acuminatis; corolla disciformi, 3 mm. diametro, petalis suborbiculatis, 1.3 cm. diametro; staminibus ca. 33, 5–8 mm. longis; disco piloso, stylo glabro, supra 1/3 diviso; stigmatibus clavatis. Capsula ignota.

CHINA: Honan: Sung Hsien, San-kian-miao, *J. Hers* 542 (A, TYPE); Yung-ning, Tsi-li-ping, *J. Hers* 402 (A).

Hers' collections were sent to the Arnold Arboretum and were named by A. Rehder as *P. incanus* (402), and *P. subcanus* Koehne (542). Hers in 1922 published the binomials accordingly. When Rehder enumerated the ligneous plants of northern China in 1924, he put both numbers under *P. incanus* and explained that the specimens under no. 542 differed in their less pubescent leaves from the type and had been tentatively referred to *P. subcanus*, but the character of the pubescence is the same as in *P. incanus*, which seems to be a very variable species. In this treatment Rehder's attention seemed to be focused chiefly on the pubescence of the leaves, and he overlooked the characters of the hypanthium and disk, which to me are more adequate for specific demarcations. The pubescence of the disk of *Hers* 542 rules out the possibility of its being *P. incanus*.

Koehne. The pubescence of the hypanthium of *P. subcanus* is short, crisp-villose, and appressed, and that of Hers' collections is long, strigose-villose, and erect. Geographically this species is out of the range of both *P. incanus* Koehne and *P. subcanus* Koehne, and morphologically it is different from them. This is a new species. The disk of *Hers* 402 is almost glabrous. It is hairy only sparingly. Aside from this, the two specimens are identical in the shape, size, and indumentum of the leaves, in the pubescence of the current year's growth, and in the nature of the hair on the hypanthium. They are from the same area.

The vernacular name "mi-tsai" can be translated as "fuel for rice," which indicates that the plants are gathered locally as fuel for cooking purposes.

40. *Philadelphus sericanthus* Koehne in Gartenfl. 45: 561. 1896; in Bot. Jahrb. 29: 371 (in Diels, Fl. Central-China). 1900, excluding *Giraldi* 1655; in Mitt. Deutsch. Dendr. Ges. 1904 (13): 84. 1904; et in Sarg., Pl. Wils. 1: 145. 1913. — Schneider, Ill. Handb. Laubh. 1: 370, fig. 236 p, 237 m-o. 1905. — Smith in Jour. Linn. Soc. Bot. 36: 500. 1905. — Stapf in Bot. Mag. 148: pl. 8941. 1922. — Rehder, Man. Cult. Trees Shrubs 274. 1927; ed. 2, 269. 1940; et Bibl. Cult. Trees Shrubs 1949. — Chen, Ill. Man. Chin. Trees Shrubs 372. 1937, pro parte. — Bean, Trees Shrubs ed. 7, 2: 419. 1950; et in Chitt., Dict. Gard. 3: 1546. 1951.

Philadelphus sericanthus var. *rosthornii* Koehne in Bot. Jahrb. 29: 371 (in Diels, Fl. Central-China). 1900.

Philadelphus sericanthus var. *rockii* Koehne, l.c.

Philadelphus coronarius var. *chinensis* Lévl., Fl. Kouy-Tchéou 389. 1916. nom. nud.

Philadelphus magdalena sensu Rehder in Jour. Arnold Arb. 12: 275. 1931, non Koehne.

LECTOTYPE: Hupei: *A. Henry* 6015 (A).

Shrub 1-3 m. high, the bark of the second year's growth gray or grayish brown, closed, longitudinally rimulose, gradually peeling off in very small pieces, the current year's growth glabrous or glabrescent. Leaves ovate-elliptic or elliptic-lanceolate, 4-11 cm. long, 1.5-5 cm. wide, obtuse or subrotundate at the base, acuminate at the apex, the acumen 8-15 mm. long, serrate, sparsely strigose or subglabrous above, sparsely strigose on the primary nerves beneath. Inflorescence 7- up to 15-flowered, rarely 5- or on weak branchlets 3-flowered; the lowest pair or pairs usually in the axils of normal leaves, the central axis glabrous or glabrescent; pedicels 6-12 mm. long, strigose, or those of the lower flowers strigose only on the apical ends; hypanthium and calyx strigose, the hairs white, not completely covering the tissue underneath; sepals ovate, 6-7 mm. long, 3 mm. wide, the apex acuminate; corolla subcampanulate disciform, 2.5 cm. across, the petals obovate, 1.3 cm. long, 1 cm. wide, sparsely strigose on the basal portion outside; stamens ca. 35, the longest 7 mm. long, the anthers glabrous; disc and style glabrous, the style 6 mm. long, the upper fourth to

half divided, the stigmata spatulate, the abaxial surface 1.5 mm. long, the adaxial slightly longer. Capsules obovoid, 7 mm. long, 5 mm. in diameter. Seed short-tailed, the embryo 1.5–1.8 mm. long, slightly longer than the tail, the testa castaneous, reticulate.

CHINA: Kiangsi: Lu-Shan, C. Y. Chiao ex Univ. Nanking Herb. no. 18553 (NY); H. H. Chung & S. C. Sun 603 (NY); Y. Tsiang 1070 (NY); A. N. Steward ex Univ. Nanking Herb. no. 2470 (MO, NY); Kiangsi-Hupei-Hunan border: Y. K. Hsiung 5600 (A), 5699 (A). Western Hupei: Pa-tung Hsien, E. H. Wilson 796 (NY), 1007 (NY); H. C. Chow 493 (A, NY); vicinity of Ichang, A. Henry 6015 (A LECTOTYPE; G, NY), 5344 (G), 7428 (G); E. H. Wilson 1282 (A, NY). Northeastern Hunan: Mo-fu-shan, Y. K. Hsiung 5149 (A). Eastern Szechuan: Ta-ning Hsien, E. H. Wilson 4496 (A); Nan-chuan, W. P. Fang 644 (A), 905 (A), 989 (A), 1063 (A, NY), 1194 (A); C. Bock & A. von Rosthorn 472 (A, ISOSYNTYPE of *P. sericanthus* var. *rosthornii* Koehne), 1918 (photo A, HOLOTYPE of *P. sericanthus* var. *bockii* Koehne), 1926 (A, ISOSYNTYPE of *P. sericanthus* var. *rosthornii* Koehne). Eastern Kweichow: Fan-ching Shan, Steward, Chiao & Cheo 609 (A, NY); San-hoa, Y. Tsiang 6451 (A, NY); Tou-chan, J. Cavalerie ex Herb. Bodinier 2343 (photo and fragment of HOLOTYPE of *P. coronarius* var. *chinensis* Lévl., A); Tuh-shan, Y. Tsiang 6633 (A); Anlung, Y. Tsiang 7433 (A). Yunnan: E. E. Maire ex Herb. Bonati 3644 (NY).

CULTIVATED: Europe: Hort. Bot. Dahlem, R. Schlechter, June, 1924 (A). United States: Arnold Arboretum, A. Rehder, June 23, 1902 (A); 4617, C. E. Faxon, June 28, 1905 (A), June 25, 1909 (A), June 21, 1910 (A) (some flowers paniculate), June 21, 1911 (A); A. Rehder, Oct. 7, 1907 (A); G. M. M., June 22, 1923 (BH). Canada: Dominion Arboretum and Botanic Gardens, Ottawa 21-69-1, J. M. Gillett, July 3, 1935 (BH).

The Vilmorin Nursery of France introduced and distributed this species to European and American gardens. The plant in the Arnold Arboretum was obtained from Vilmorin, and that in the botanic garden at Ottawa was received from the Royal Botanic Gardens at Kew.

Koehne cited three specimens, designating no type. *Henry 6015* is here selected as the lectotype.

Koehne in 1900 on the basis of C. Bock and A. von Rosthorn's collection from Manchuan, southwestern Szechuan, described two varieties. *Philadelphus sericanthus* var. *bockii* Koehne was established on the strength of the smaller leaves and flowers. The photograph of the type (Rosthorn 1918) indicates that the material was collected from a much-branched old growth, which naturally produces smaller leaves and flowers. I can see no reason for keeping it as a variety. *Philadelphus sericanthus* var. *rosthornii* Koehne was published on the basis of *Bock & Rosthorn 1919, 1926, 1927*, and 472. In the original description Koehne did not list a single stable character for the variety. Not only does every statement allow for variation, but also most of the statements contain alternatives. Before me are *Bock & Rosthorn 472* and 1926. The latter is flowering material. It is identical with *Henry 6015*, a lectotype of *P. sericanthus* Koehne. *Bock & Rosthorn 472* is a fruiting specimen. The compressed hairs on its leaves suggest *P. henryi* Koehne.

Philadelphus sericanthus Koehne is endemic to Central China, with the famous Wu-Shan as the center of its range. Hence its range extends westward to eastern Szechuan, where it has been recorded from Ta-ning and Man-chuan districts, southward to eastern Kweichow, and southeastward to the Kiangsi-Hupei-Hunan border. Material from the periphery of this range has a more strigose upper leaf surface than the typical specimens. It is a shrub occurring in lightly shaded woods or thickets at altitudes of 500–1000 meters. Most field notes record it as one to three meters high. Steward, Chiao, & Cheo have recorded it as a tree five meters high with a trunk fifteen cm. in diameter. If this observation was made by either Steward or Chiao, I must accept the fact that some members of the genus *Philadelphus* are trees. However, knowing that there is no arborescent form in this genus, it is probably safe to assume that this observation was a mistake on the part of Cheo, whose botanical knowledge is limited.

Up to the present I have not learned the vernacular name of this species. No collector has ever recorded it. Chen in 1937 tried to assign a Chinese name to it. Léveillé published *P. coronarius* Linn. var. *chinensis* Lévl. on the basis of J. Cavalerie's collection ex Herb. Bodinier no. 2343. Rehder saw the holotype of this trinomial and interpreted it as a glabrescent form of *P. magdalena* Koehne. Typical *P. magdalena* has a pubescent disk and leaves which are uniformly pubescent on both surfaces. Cavalerie's specimen has a glabrous style and disk and leaves glabrous except on the primary nerves beneath. It is a typical *P. sericanthus* Koehne. *Tsiang 6451* in the New York Botanical Garden has paniculate inflorescences, while that in the Arnold Arboretum has racemose ones. This is another illustration of the tendency toward branching of the lower elements of the inflorescences of the genus.

This species was introduced into western gardens by Father Farges, who was stationed in Cheng-Kou (Tschen-Kéu) of eastern Szechuan and who collected plants, specimens, and seeds for French institutions. In 1897 Farges' seed reached M. L. de Vilmorin, who numbered it 7183. From this lot the Arnold Arboretum obtained a plant in 1902, which marked the date of the introduction of this species into the New World. Bean recorded its introduction into England by Wilson in 1900. I have not seen any cultivated material of this introduction. At the Arnold Arboretum it flowers in the latter part of June. Cultivation does not seem to affect the size of the flower or the nature of its indumentum. Besides its late flowering period it warrants little merit. The flowers are small and the habit stiff.

40a. *Philadelphus sericanthus* var. *kulingensis* (Koehne) Hand.-Mazz., Symb. Sin. 7: 439. 1931.—Chen, Ill. Man. Chin. Trees Shrubs 372. 1937.

Philadelphus incanus var. *sargentianus* forma *kulingensis* Koehne in Fedde, Repert. Nov. Sp. 10: 126. 1911; et in Sarg. Pl. Wils. 1: 145. 1912.

Philadelphus sericanthus var. *rehderianus* sensu Cheng in Contr. Biol. Lab. Sci. Soc. China Bot. 10: 114. 1936, non Koehne.

Philadelphus sericanthus sensu Chen, Ill. Man. Chin. Trees Shrubs 372. 1937, non Koehne.

TYPE: Kiangsi: *E. H. Wilson* 1669 (A).

An erect shrub, the second year's growth brownish gray, the bark closed, longitudinally rimulose, the current year's growth glabrous or glabrescent; leaves ovate-elliptic, 5–8.5 cm. long, 2.5–4 cm. wide, acute or obtuse at the base, acuminate at the apex, the acumen 5–10 mm. long, sharply and prominently serrate, 9–12 teeth on each side, glabrous above, sparsely pilose on the principal nerves or on the nerves and veinlets beneath; inflorescence 7-, 9-, or 11-flowered; pedicels glabrous, 10–25 mm. long; hypanthia and sepals partially and sparsely pilose, the hairs appressed; capsules obovoid, 7–9 mm. long, 6–7 mm. in diameter.

CHINA: Chekiang: Hang-chow, *E. D. Merrill* 11271 (A). Kiangsi: Kuling, *E. H. Wilson* 1669 (A, TYPE); Lu-shan, *H. H. Chung & S. C. Sun* 215 (NY), 396 (A, NY).

This variety differs from the typical *P. sericanthus* in having partially pubescent hypanthia and sepals. In the reduction of the density of hairs on the hypanthia this variety approaches *P. brachybotrys* var. *laxiflorus* (Cheng) S. Y. Hu. Cheng in 1936, on the basis of *M. Chen* 649, *K. K. Tsoong* 366, and *S. Chen* 212, reported *P. sericanthus* var. *rehderianus* Koehne to occur in western Chekiang. Koehne's trinomial was based on a plant collected on the high plateaus of Sung-pan in western Szechuan. Although I have not seen any of these three specimens, from a phytogeographical point of view the material of the maritime province Chekiang cannot be identical with that of the Sino-Tibetan plateau. Very likely Cheng's material belongs here, as western Chekiang supports a flora similar to that of the Central Yangtze Basin, where Kuling is located.

41. *Philadelphus henryi* Koehne in Fedde, Rep. Sp. Nov. 10: 126. 1911.—Lévl., Cat. Pl. Yunnan 255. 1917.—Rehder in Jour. Arnold Arb. 12: 275. 1931.—Hand.-Mazz., Symb. Sin. 7: 437. 1931.

Philadelphus nepalensis sensu Lévl., Cat. Pl. Yunnan 255. 1917, non Koehne. *Deutzia mollis* var. *erythrocalyx* Lévl. ex Rehd. in Jour. Arnold Arb. 12: 275. 1931, in syn.

LECTOTYPE: *A. Henry* 10749 (A).

A shrub 1.5–2.5 m. high, the bark of the second year's growth castaneous, closed, tardily exfoliate, the current year's growth crisp-hirsute. Leaves ovate or rarely ovate-lanceolate, 3.5–8 cm. long, 1.5–4 cm. wide, rounded or obtuse at the base, acuminate at the apex, the acumen 5–15 mm. long, sparsely or uniformly scabrid above, scabrid-strigose on the primary nerves or veinlets beneath, subentire or faintly denticulate, rarely serrate. Inflorescence 5- up to 22-flowered, rarely on weak branchlets 1-flowered,

racemose, rarely paniculate, the rachis 3–9 cm. long; pedicels 4–5 mm. long, densely scabrid; hypanthium and calyx crisp-pilose, the underlying tissue visible; sepals ovate, lanceolate, rather sparsely pilose; corolla subdisciform, 2.5–3 mm. across, the petals oblong, 1.3 cm. long, 8–11 mm. wide, the back glabrous; stamens ca. 38, the longest 7 mm. long, the anthers oblong, the disc and style glabrous, 5.5 mm. long, the stigma oar-shaped, the abaxial surface 2 mm. long, the adaxial narrower, slightly longer or almost wanting. Capsules obovoid; 6 mm. long, the apical end 6 mm. in diameter, the persistent calyx subapical. Seed short-caudate, the testa castaneous, reticulate, the embryo 1.5 mm. long, the tail 1.5 mm. long.

CHINA: Southwestern Szechuan: Ma-pien Hsien, *F. T. Wang* 23017 (A); Wa-shan, *E. H. Wilson* 3040 (A); Minya Konka Snow Range, east of Yu-long Hai, *J. F. Rock* 17624 (A, NY). Yunnan: Mengtze, *A. Henry* 10749 (A, LECTOTYPE; NY), 10749A (MO, NY, US), 10749B (A); Pé-long-tsien, *E. E. Maire* (A, HOLOTYPE of *Deutzia mollis* var. *erythrocalyx* Lévl. ex Rehder); Kun-ming (Yunnanfu), *O. Schoch* 148 (A, US); Cheng-kiang, *Y. Tsiang* & *H. Wang* 16141 (A); Cheng-kang Snow Range, *T. T. Yu* 16951 (A); Yang-ki, *McLaren*, *C. collection* 138 (A); Ping-pien Hsien, *H. T. Tsai* 62399 (A); Ta-li Range, *G. Forrest* 5032 (A).

This species was first recorded from Mengtze in southwestern Yunnan. Representatives from central and western parts of that province have been collected in recent years. *Wang* 23017 extends its range far north into southwestern Szechuan. It has an altitudinal range of 1500–3380 meters. The specimens collected from western Yunnan resemble *P. delavayi* L. *Henry* in vegetative characters and in the form of the stigma. It is because of their pubescent hypanthia that they are placed here. In Yunnan the white flowers of this species appear as early as May in the southwest part of the province and as late as July in the northeast.

In his original description Koehne cited *A. Henry* 10749 and 10749B, without designating a type. In the herbarium of the Arnold Arboretum a detailed note in Koehne's handwriting is attached to 10749, and this specimen is selected as the lectotype.

Diels named *Forrest* 5032 *P. nepalensis*. This specimen in the herbarium of the Arnold Arboretum has pubescent hypanthia and leaves. It is different from the glabrous Himalayan species. *Wilson* 1772, cultivated in the Arnold Arboretum, flowered in June 1910. It appears to belong here.

41a. *Philadelphus henryi* Koehne var. *cinereus* Hand.-Mazz., Symb. Sin. 7: 438. 1931.

Philadelphus cinereus Hand.-Mazz. in Karsten & Schenck, Vegetationst. 20 (7): [15]. 1930, nom. nud.; et Symb. Sin. 7: 438. 1931, in syn.

TYPE: Yunnan, *Handel-Mazzetti* 6181 (Vienna).

A shrub up to 3 m. high, the current year's growth cinereo-hirtellous; leaves ovate-lanceolate or ovate on vegetative shoots, 3.5–6 cm. long, 1–3 cm. wide, obtuse at the base, acuminate rarely acute at the apex, subentire

or faintly denticulate, uniformly scabrid-strigose on both surfaces; inflorescence 7- up to 17-flowered, racemose or often paniculate; pedicels, hypanthia and calyx cinereous, crisp-villose; corolla subdisciform, 2.5 cm. across, the petals suborbicular, 1.1 cm. in diameter.

CHINA: Yunnan: Chen-hsiung Hsien, *H. T. Tsai* 52244 (A); central Yunnan, Lo-shiuek Mts., *McLaren's collectors*, *U* 137 (A); La-pa-ho, *Siméon Ten* 195a (A); Yung-ning-Yung-peh, *C. Schneider* 3505 (A).

42. *Philadelphus tenuifolius* Rupr. ex. Maxim. in *Bull. Phys.-Math. Acad. Sci. St. Pétersb.* 15: 133. 1856; et in *Mél. Biol.* 2: 425. 1857.—Rupr. in *Bull. Phys.-Math. Acad. St. Pétersb.* 15: 365. 1857.—Maxim., *Prim. Fl. Amur.* 108. 1859.—Koehne, *Deutsche Dendr.* 182. 1893; in *Gartenfl.* 45: 597. 1896; et in *Mitt. Deutsch. Dendr. Ges.* 1904(13): 84. 1904.—Forbes & Hemsl. in *Jour. Linn. Soc. Bot.* 23: 278. 1887.—Schneider, *Ill. Handb. Laubh.* 1: 372. 1905.—Yabe, *Icon. Fl. Manch.* 1: *pl.* 18. 1920.—Minami, *List Pl. Manch. Mong.* 183. 1926.—Nakai, *Chosen-shokubutsu* 1: 335, *fig.* 413. 1914; in *Bot. Mag. Tokyo* 29: 64. 1915; et *Fl. Sylv. Kor.* 15: 52. 1926.—Nekrasowa, *Fl. As. Russ.* I. 3: 3. 1924.—Chen, *Ill. Man. Chin. Trees Shrubs* 374. 1937.—Poiarkova in *Komarov, Fl. SSSR* 9: 221, *pl.* 13, *fig.* 1. 1939.—Kitagawa, *Lineam. Fl. Mansh.* 253. 1939.—Rehder, *Man. Cult. Trees Shrubs* 276. 1927; ed. 2, 270. 1940; et *Bibl. Cult. Trees Shrubs* 193. 1949.

Philadelphus coronarius var. *tenuifolius* Maxim. in *Mém. Acad. Sci. St. Petersb.* VII. 10(16): 38 (Rev. Hydrang. As. Or.). 1867.—Dippel, *Handb. Laubh.* 3: 336. 1893.

Philadelphus coronarius sensu Regel, *Tent. Fl. Ussur.* 62. 1861, non *Linn.*

Philadelphus tenuifolius forma *subinteger* Komarov in *Bull. Jard. Bot. Russe* 16: 172. 1916.—Nekrasowa, *Fl. As. Russ.* I 3: 4. 1924.

Philadelphus tenuifolius forma *dentata* Komarov, l.c.—Nekrasowa, l.c.

Philadelphus tenuifolius forma *multiflorus* Komarov, l.c.

Philadelphus viksnei Zamelis in *Acta Hort. Bot. Univ. Latv.* 11-12: 232, *pl.* 1. 1939.

Philadelphus robustus Nakai in *Jour. Jap. Bot.* 19: 372. 1943.

TYPE: *Ruprecht* (Herb. Acad. Sci. USSR).

An upright shrub 1-3 m. high, with arching branches, bark of the second year's twigs brownish gray, rarely chestnut-brown, moderately exfoliate; the current year's growth pubescent, the hairs compressed. Leaves on the vegetative shoots ovate, up to 10.5 cm. long, 6 cm. wide, remotely dentate, sparsely villose on the primary nerves and at their angles beneath, otherwise glabrous, the base acute, obtuse or rarely roundish; the apex abruptly short-acuminate; leaves of the flowering twigs ovate or elliptic, 4-6.5 cm. long, 2-3 cm. wide, glabrescent and barbate beneath, very sparsely pilose above, acute, obtuse or roundish at the base, acute or short-acuminate at the apex, remotely serrate or subentire. Flowers

slightly fragrant, 5 or 7 (rarely 3 or 9) in a raceme, the pedicels rather long, usually longer than the hypanthium plus the calyx, densely pubescent, the sepals ovate, 5 mm. long, sparsely pubescent; corolla 2.5 cm.-3.4 cm. across, the petals obovate-oblong, 1-1.5 cm. long, 0.6-1 cm. wide; stamens 25-30; style and disk glabrous, the style half divided, the abaxial stigmatic surface equal to or half the length of that of the adaxial one. Capsules obconic, rounded at the apical end, 4.5-6 mm. long, 5 mm. in diameter, the persistent sepals subapical. Seeds short-caudate.

EASTERN SIBERIA: Amur: Korfowskaja, *S. J. Enander*, Aug. 3, 1913 (A). Manchuria: Er Tieng Tien Tze, *P. H. Dorsett* 3059 (A); Kirin, *F. H. Chen* 263 (A).

KOREA: *K. G. Gilbert* 57 (A); Taiyudo, French mine, *E. H. Wilson* 8635 (A, US); South Keisho, Chirisan, *E. H. Wilson* 9619 (A); Keiki, Keijyo, *E. H. Wilson*, May 13, 1914 (A); Tsü-sima Island, *C. Wilford* 1859 (G).

CULTIVATED: Europe: Hort. Bot. Berol., *E. Koehne* 364 (A, G); Royal Bot. Gard., Edinb., *D. Drysdale*, June 19, 1929 (A). United States: Arnold Arboretum 4654, without collector, in 1904 (A), *S. Y. Hu*, June 13, 1951 (A).

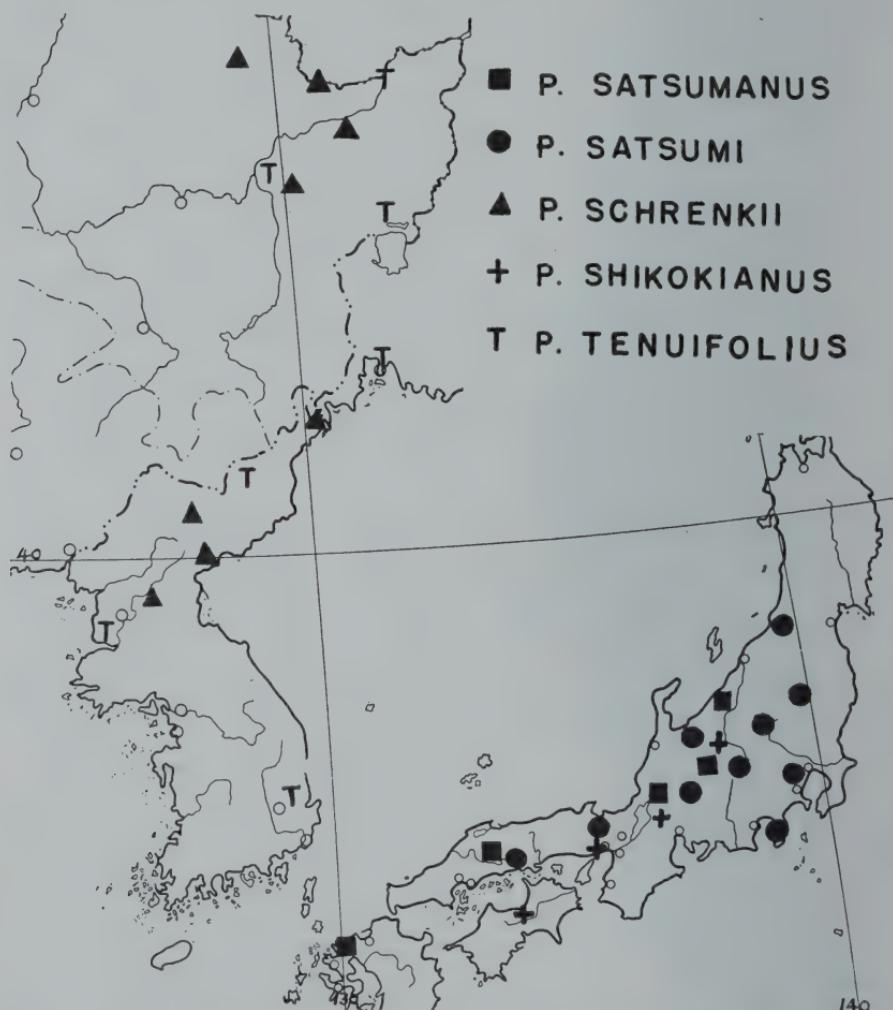
The natural range of this species is the valley of the Amur River and its tributaries, the Sungari and Ussuri Rivers, hence southward to Vladivostok and South Korea (Map 6). In its natural home it is a very common bush at altitudes of 150 to 900 m. It flowers in mid-June, the flowers being slightly fragrant.

Ruprecht and Maximowicz differentiated their species from *P. coronarius* Linn. by their smaller size, weaker branches, cinereous bark, submembranaceous and deeper green leaves, smaller and inodorous flowers, and subundulate petals. They compared the spontaneous *P. tenuifolius* of the Amur River region, where it was subjected to long continued cold weather, with the cultivated *P. coronarius* of the European gardens. But the living specimens of the two species growing side by side in the Arnold Arboretum do not exhibit any appreciable differences in habit, size of branches, or even in the texture of the leaves. The brownish gray bark of the two-year-old growth, the compressed hairs on the lower surface of the leaves, the faint fragrance of the flowers, and the short-tailed seeds are distinguishing characters of *P. tenuifolius*. In its seed characters this species seems to be closer to *P. pekinensis* than to *P. coronarius*.

Zamelis' description of *P. viksnei* was based on a plant raised from seed collected in Vladivostok. He distinguished it from *P. tenuifolius* by its "statura erecta, foliis floribusque majoribus." The photograph of the type plant appears to resemble the *P. tenuifolius* in our garden. Judging from the published notes of the hybridization work he did with Pochlaks, there seems to be no *P. tenuifolius* in the botanical garden of the University of Latvia. Possibly Zamelis did not have the true *P. tenuifolius*, and his comparison of the habit of his new entity, including the leaf and flower sizes, with *P. tenuifolius* may have been derived from books, perhaps from Maximowicz' observations. Since cultivation inevitably changes the aspect of a plant, the better soil and care in the garden often resulting in larger plants, and as Vladivostok is within the natural range of distribution of

P. tenuifolius, I see no reason for keeping *P. viksnei* as a distinct species.

Komarov described three forms on the basis of the number of teeth on the leaf margin and the number of flowers in the inflorescence. He designated specimens with more or less entire leaves as forma *subinteger*, those with ten to twenty teeth as forma *dentatus*, and those with nine to eleven



MAP 6. The distribution of the species of *Philadelphus* in northeastern Asia and Japan.

flowers as forma *multiflorus*. Arnold Arboretum no. 4654 was introduced from Germany in 1902. Specimens collected in 1904 have thick two-year-old branches bearing many flowering twigs. This plant has been propagated vegetatively from time to time. In 1951 these plants showed signs of debility. There were no thick branches bearing a large number of

flowering twigs. Moreover, each flowering twig bore only one, two, or three flowers. The leaves of the few small virgin shoots are dentate, as are those collected in 1902. This plant is a good illustration of the variation of the leaf-margins, the number of teeth varying with the age and vitality of the plant. The number of flowers on a flowering twig seems to tell the same story. For this reason there seems to be no valid reason for accepting Komarov's three forms.

42a. *Philadelphus tenuifolius* var. *latipetalus*, var. nov.

Frutex erectus; foliis ovatis, usque ad 11 cm. longis et 6 cm. latis, basi rotundatis vel obtusis, apice acuminatis; margine denticulatis; racemis 5- vel 7-floris, floribus 3 cm. diametro, petalis suborbiculatis, 8 mm. diametro; stylo et disco glabris.

MANCHURIA: B. V. Skvortzov, June 6, 1925 (TYPE, A).

This variety differs from typical *P. tenuifolius* chiefly in its suborbicular petals, which result in a discoid appearance of the corolla.

43. *Philadelphus subcanus* Koehne in Mitt. Deutsch. Dendr. Ges. 1904(13): 83. 1904; et in Sargent, Pl. Wils. 1: 4. 1911. — Dunn in Jour. Linn. Soc. Bot. 39: 475. 1911. — Rehder, Man. Cult. Trees Shrubs 274. 1927; ed. 2, 268. 1940; et Bibl. Cult. Trees Shrubs 192. 1949. — Engler, Pflanzenf. ed. 2, 18a: 194. 1930. — Chen, Ill. Man. Chin. Trees Shrubs 372. 1937.

Philadelphus wilsonii Koehne in Sargent, Pl. Wils. 1: 4. 1911, 1: 145. 1912. — A. O[sborn] in Gard. Chron. III. 114: 186, fig. 93. 1943.

Philadelphus subcanus var. *wilsonii* (Koehne) Rehder in Jour. Arnold Arb. 1: 196. 1920; Man. Cult. Trees Shrubs 274. 1927; ed. 2, 268. 1940; et Bibl. Cult. Trees Shrubs 192. 1949. — Chen, Ill. Man. Chin. Trees Shrubs 372. 1937. — Bean in Chitt., Dict. Gard. 3: 1546. 1951.

Philadelphus sericanthus var. *rehderianus* Koehne in Fedde, Repert. Nov. Sp. 10: 127. 1911; et in Sarg., Pl. Wils. 1: 145. 1912. — Chen, Ill. Man. Chin. Trees Shrubs 372. 1937.

Philadelphus paniculatus Rehder in Jour. Arnold Arb. 11: 159. 1930.

TYPE: Szechuan, A. Henry 8823.

A stiff erect shrub 3-6 m. high; the second year's growth brown or grayish brown, the bark closed, tardily exfoliating, the current year's growth brown, glabrous or glabrescent. Leaves ovate or ovate-lanceolate, 4-14 cm. long, 1.5-7 cm. wide, rounded or obtuse at the base, acuminate at the apex, the acumen 0.5-1.5 cm. long, faintly denticulate or those on the vegetative shoots finely serrate, sparsely hirsute above, the hairs erect, villose on the nerves beneath. Inflorescences essentially racemose, occasionally on vigorous shoots paniculate, 5- up to 25-flowered, generally 9- or 11-flowered, the rachis 2.5-22 cm. long, villose and glabrescent; the peduncles of individual cymes, when present, 6-12 mm. long, the pedicels 5-10, rarely up to 13 m. long, densely crisp-villose; hypanthium and

calyx crisp-villose, the hairs grayish yellow with the underneath tissue visible; sepals ovate, 6–7 mm. long, 3–4 mm. wide, the apex acuminate; corolla disciform, 2.5–3, rarely up to 4 cm. across, the petals suborbicular or obovate, rarely ovate, 1.3–1.8 cm. long, 9–1.3 cm. wide, generally setose on the lower portion of the back; stamens about 33, the longest 9–10 mm. long; disc pubescent, the style 6 mm. long, the lower portion pubescent, the stigmata subspatulate, the abaxial surface 1.5–2 mm. long, the adaxial equal but obscure, or wanting. Capsules obovoid, 8–10 mm. long, 6 mm. in diameter, the persistent calyx subapical. Seeds very short caudate, the testa brown, the embryo 1.5 mm. long, the tail one fourth as long, the lobes of the crown rounded.

CHINA: Szechuan: Mao Hsien, F. T. Wang 21910 (A); Kuan Hsien, W. P. Fang 2237 (A, TYPE of *P. paniculatus* Rehd.), 2349 (A); same area, Pan-lun Shan, E. H. Wilson 4297 (A); Wen-chuan, Wa-ssu County, E. H. Wilson 3041 (A, TYPE of *P. wilsonii* Koehne), 3043 (A); Li-fan, F. T. Wang 21564 (A); Mao-kung Hsien, F. T. Wang 21274 (A); Juei-she Hsien, T. T. Yu 1037 (A); Mt. Omei, C. Y. Chiao & C. S. Fan 554 (A); W. P. Fang 2799 (A), 6738 (A), 12837 (A); Y. S. Liu 1208 (A), 1474 (A), 7622 (A, NY); C. L. Sun 351 (BH); F. T. Wang 23344 (A); E. H. Wilson 4883 (A); Sung-pan, H. Smith 2741 (A); without precise locality, W. P. Fang 6728 (NY). Sikang: (Western Szechuan): Mu-pin, E. H. Wilson 3039 (A); Tai-chien-lu, E. H. Wilson 3042 (A), 4384 (A); Minya Konka Snow Range, east of Yu-long Hai, J. F. Rock 17624 (A, NY, US). Yunnan: Pin-chuan Hsien, H. T. Tsai 52974 (A).

CULTIVATED: Arnold Arboretum 7828-1 = 6529 = Wilson 1247, without collector, 1911 (A); Arnold Arboretum 312-29, E. R. Sears, June 21, 1935 (BH); Highland Park, Rochester, N.Y., R. E. Horsey, May 31, 1918 (BH); Borderland, North Easton, Mass., Oaks Ames, June 23, 1917 (BH).

Koehne established *P. subcanus* on the basis of *A. Henry* 8823, a specimen collected from Szechuan. I have not seen the type of this species. According to Koehne, it has a dark brown current year's growth which becomes glabrous at anthesis; ovate leaves 4.5–11.5 cm. long, 2.2–8 cm. wide, with short scattered hairs above and rather dense hirsute hairs on the nerves beneath; hypanthium with grayish yellow tomentum and short crisp hairs; small flowers 2.2 cm. in diameter with orbicular petals; about 30 stamens and style pubescent below the middle.

Before me there are four specimens of Wilson's western Szechuan collection, nos. 3039, 3042, 3043 and 4883, which were named by Koehne as *P. subcanus*. These specimens fit well Koehne's description in the above-mentioned characters. No. 3043 from Wen-chuan and no. 4883 from Mt. Omei have almost glabrous petals. No. 3039 from Mu-pin evidently has golden setose hairs at the base on the outside of the petals. No. 3042 from Ta-chien-lu consists of three fragments in the Arnold Arboretum. One of these has glabrous petals, another has distinctly golden setose petals, and the third is intermediate, with most petals glabrous and some inconspicuously setose. This specimen also exhibits a considerable variation in the shape and size of the leaves. Take the largest leaves of different flowering twigs on the same branchlet for comparison — in shape they vary from

ovate to lanceolate and in size from 9 cm. long and 3.5 cm. wide to 5 cm. long and 1.5 cm. wide. The largest leaf of a vegetative shoot on the same sheet is 13 cm. long and 7.3 cm. wide.

In 1911 Koehne established *P. wilsonii*, based on a specimen collected by Wilson in Wen-chuan. In a note he remarked that this species is allied to *P. subcanus*, from which it differs chiefly in the unusually large leaves on the flowering shoot. The type of this species, *Wilson 3041*, was apparently collected from a vigorously growing plant, and consequently it has larger leaves. But such large leaves are not confined to this collection. *Wilson 3042*, which was named *P. subcanus* by Koehne also has leaves reaching similar size. In the nature of the indumentum and the flower characters, *Wilson 3041*, the type of *P. wilsonii* Koehne, is identical to the above-mentioned Wilson numbers, especially 3039. On the basis of the morphological similarities and geographical distribution all these specimens should belong to one species, and *P. subcanus* Koehne has priority.

Another species from the general area was published by Rehder in 1930 on the strength of its paniculate inflorescences. Rehder maintained that that species, *P. paniculatus*, seems to be most closely related to *P. sericanthus* Koehne and *P. subcanus* Koehne. The type of this species, *W. P. Fang 2237*, from Kuan-Hsien, is a fruiting specimen. Compared with the above-mentioned Wilson collection, the hairs on the nerves of the lower surface are more scattered. But the age of the leaves may account for such reduced density of indumentum. The infructescences of this specimen are paniculate. This condition is not uncommon among the *Philadelphus* species of West China. The vigorously growing branches of a species that normally bears racemose inflorescences often produce paniculate ones. For example, *Wilson 3043* from Wen-chuan has largely racemose inflorescences, but the pedicels of the lowest pairs of flowers of one of them tend to branch and give rise to cymes. *Wilson 4384* from Ta-chien-lu has two flowering twigs. The lower one has eleven flowers in a normal racemose arrangement and the upper one on the same branchlet has nineteen flowers arranged in a paniculate pattern. This specimen was named *P. wilsonii* by Koehne, and later it was changed to *P. subcanus* var. *wilsonii* (Koehne) Rehder. If the paniculate portion of this specimen should be cut off and placed on *Fang 2237*, the type of *P. paniculatus* Rehd., there would be no reason for anybody to suspect that these elements were from two different collections. Furthermore, Wen-chuan Hsien, the type locality of *P. wilsonii* Koehne, and Kwan Hsien, the type locality of *P. paniculatus* Rehder, are adjacent counties in northwestern Szechuan, situated at the point where the Min River emerges from the rugged mountains. That area I know best, for I spent five summers traveling through it studying the vegetation and collecting plant specimens. From a phytogeographical point of view the localities where the types of *P. wilsonii* Koehne and *P. paniculatus* Rehder were collected are in one inseparable unit. They support the same type of vegetation. Both morphological and geographical evidence indicate that *P. paniculatus* Rehder and *P. wilsonii* Koehne are conspecific, and in my opinion they are both synonymous with *P. subcanus* Koehne.

The crisp golden hairs on the capsules of the type of *P. sericanthus* var. *rehdelianus* Koehne clearly indicate that this material is a fruiting specimen of *P. subcanus*. Koehne established this trinomial on the strength of the large ovate leaves which are glabrous above. The data on the label of this material say that the specimen was collected in October. Sung-pan, the type locality of this trinomial, is situated on the high plateau of north-western Szechuan; the general altitude is 2740 meters. Its growing season is short. Thus the leaves on this specimen are falling, and those left on the plant are too old to show adequately the characters of their pubescence. I can see no reason for keeping that variety under *P. sericanthus*.

The description of the seed is drawn from *Wilson* 4384 from Ta-chien-lu. *Chiao & Fan* 554 from Mt. Omei has seeds with longer tails, which are as long as the embryos. *Philadelphus subcanus* Koehne is a species of western Szechuan. Its range extends from the Chun-lai Range westward to eastern Sikang up the highlands of Ta-chien-lu, and southward to northern Yunnan as far as Long. $100^{\circ} 35'$ E. and Lat. $25^{\circ} 44'$ N. The indumentum on the leaves and the type of stigma suggest a close relationship with *P. henryi* Koehne. The latter species has a glabrous style. In western Szechuan this species grows in forests at altitudes of 1850–3050 meters. It has been recorded as a shrub from two to six meters high. The white flowers appear in June. E. H. Wilson introduced this species to the Arnold Arboretum and the Vilmorin Nursery in 1908. The plant in the Arnold Arboretum flowered in 1911.

KEY TO THE VARIETIES OF *P. subcanus*

- A. Hypanthia villose sublanate; base of the back of the corolla pilose. a. var. *dubius*.
- AA. Hypanthia weak villose, the hairs crisp; back of the corolla glabrous. b. var. *magdalenae*.
- 43a. *Philadelphus subcanus* var. *dubius* Koehne in Sargent, Pl. Wils. 1: 4. 1911.

LECTOTYPE: Szechuan, *Wilson* 4044 (A).

Shrub 1.5–3 m. high, bark of the second year's growth brown, tardily exfoliate; the current year's growth villose, the hair crisp. Leaves ovate, 2–7.5 cm. long, 1.5–3.5 cm. wide, on sterile shoots up to 9 cm. long, 5 cm. wide, rounded or obtuse at the base, acute or shortly acuminate at the apex, serrate, hirsute above, uniformly villose-sublanate beneath; inflorescences 7- or 9-flowered, the pedicels, hypanthium and calyx long-villose-sublanate; flowers disciform, 2.5 cm. across, the petals suborbicular, nearly glabrous outside with a few hairs at the base; stamens about 30; base of style with a few weak white hairs.

CHINA: Szechuan: West of Wan Hsien, Pan-lan-Shan, *Wilson* 4044 (A, TYPE).

This variety is known only from the type collection. Koehne recognized it as a variety on the strength of the constant loosely pilose stems below

the inflorescences and the dense pilose lower surface of the leaves. It seems to me that the long-villous nature of the indumentum on the hypanthium adds a more readily distinguishable character to this distinctive variety. In the typical form of *P. subcanus* Koehne the hairs on the hypanthium are weak, short, and crisp.

43b. *Philadelphus subcanus* var. *magdalena* stat. nov.

Philadelphus magdalena Koehne in Mitt. Deutsch. Dendr. Ges. 1904 (13): 83. 1904; 1906 (15): 53. 1906; et in Sargent, Pl. Wils. 1: 145. 1912.— Vilmorin et Bois, Frutic. Vilmor. 129. 1904.— Schneider, Ill. Handb. Laubh. 1: 369. 1905.— Silva Tarouca, Freiland-Laubgehölze 283, fig. 352. 1913; 256, fig. 308. 1930.— Rehder, Man. Cult. Trees Shrubs 274. 1927; ed. 2, 268. 1940; et Bibl. Cult. Trees Shrubs 192. 1949.— Bean in Chitt. Dict. Gard. 3: 1546. 1951.

TYPE: Vilmorin 7182 (cultivated, seed from Szechuan, China).

Shrub up to 4 m. high, the bark of the second year's growth grayish brown, tardily exfoliate; current year's growth sparsely villous or glabrescent. Leaves ovate, 3–6 cm. long, 1–3 cm. wide, rounded at the base, shortly acuminate or acute at the apex, uniformly pubescent on both surfaces, scabrid or hirsute above, the hairs erect, scabrid-villous beneath, the hairs more or less appressed. Inflorescence 5- up to 11-flowered, racemose or in a few cases paniculate; pedicels, hypanthium and calyx weak-villous, the hairs crisp, the tissue beneath visible; corolla subdisciform, 2 cm. across, the petals glabrous on the back, stamens about 28; style pubescent; capsules ovoid, 10 mm. long, 7 mm. in diameter, the persistent sepals attached a little above the middle; seeds short-caudate, the testa castaneous, the tail slightly shorter than the embryo.

CHINA: Szechuan [Sikang]: Raurong to Ta-chien-lu via Hadjaha, H. Stevens 150 (A); Ta-chien-lu uplands, E. H. Wilson 4337 (A), 4387 (A). Yunnan: without precise locality, E. E. Maire 401 (A); rochers de Pe-longtsin, E. E. Maire 3354 (NY, US).

CULTIVATED: Europe: Hort. Vilmorin 2182, Herb. Dendr. C. Schneider, June 6, 1906 (from TYPE plant. A). United States: Arnold Arboretum 5315-1, without collector, June 13, 1918 (BH).

Philadelphus magdalena Koehne was established on the basis of a plant cultivated under the number 7182 in the garden of M. L. de Vilmorin, Les Barres, France. The seed was originally collected by Farges in 1894 in Szechuan. It germinated in 1895, and by the time of the publication of the species the type plant was nine years old. Before me there is a specimen collected from that plant on June 2, 1906. It indicates that the plant had not been cared for properly. It is in a declining stage. Most of the flowering twigs were developed from adventitious buds. Consequently the leaves are small and the hairs appear unusually dense. As seen through a binocular, the hairs on the under surface of the leaves are all on the veins and veinlets in the same manner as are the hairs of the under surface of typical *P. subcanus* Koehne. It is the smaller size of the area enclosed

by the reticulations that makes the indumentum appear unusually dense. The inflorescences of this specimen are racemose with some pedicels of the lower flowers tending to branch and to produce cymes in place of single flowers. The petals of this specimen are glabrous. As exhibited in *Wilson* 3043, 4883, 3042 and 3039, there is considerable variation in the pubescence on the petals in the typical *P. subcanus* Koehne, from glabrous to evidently golden setose. To me this character is not sufficiently reliable to warrant specific rank, and so it is treated as a variety of *P. subcanus* Koehne with small and uniformly pubescent leaves and glabrous petals.

This variety resembles *P. henryi* var. *cinereus* Hand.-Mazz. in its small, uniformly pubescent leaves, but the latter taxon has a glabrous style and disk.

E. E. Maire 3354 in the New York Botanical Garden has a pubescent style and disk. It definitely belongs here. But the material deposited in the Arnold Arboretum with identical field notes but no number has a glabrous style and disk. Rehder considered that specimen to be *P. henryi* Koehne, and he was right.

44. *Philadelphus kansuensis* (Rehder), stat. nov.

Philadelphus pekinensis var. *kansuensis* Rehder in Jour. Arnold Arb. 9: 49. 1928; Man. Cult. Trees Shrubs ed. 2, 270. 1940; et Bibl. Cult. Trees Shrubs 193. 1949.—Walker in Contr. U. S. Nat. Herb. 28: 626. 1941.

TYPE: Kansu, *J. F. Rock* 12587 (A).

Upright shrub 2–7 m. high; bark of second year's growth grayish brown, exfoliate, the current year's growth glabrescent or sparsely crisp-villose. Leaves ovate or ovate-lanceolate on the vegetative shoots, up to 11 cm. long, 6.5 cm. wide, on the flowering shoots usually 3–5 cm. long, 1–2 cm., rarely up to 3 cm. wide, subentire or faintly serrate, obtuse or rounded at the base, acuminate at the apex, strigose-villose on the primary nerves and sometimes on the veinlets beneath, rather uniformly setose above, the hairs on both surfaces more or less erect. Inflorescences 5-, 7-, or rarely up to 11-flowered; the rachis 2–8 cm. long, sparsely crisp-villose; pedicels 6–8 mm. long, grayish strigose-villose, the hairs suberect; hypanthium and calyx sparsely strigose-villose, the hairs thickened at the base; sepals ovate-deltoid, 4 mm. long, 3 mm. wide, the apex acute or acuminate; corolla subdisciform, 2.5 cm. across, the petals oblong-suborbicular, 1.2–1.5 cm. long, 1–1.3 cm. wide, sparsely weak-villose at the base on the back; stamens ca. 28, the longest 9 mm. long; disc setose at the rim, otherwise glabrous, the style glabrous, 6–7 mm. long, the upper fifth divided, the stigmas 3 or 4, clavate, the abaxial surface 1 mm. long, the adaxial longer and narrower. Capsules obovoid, 6–8 mm. long, 4–5 mm. in diameter, the persistent sepals subapical. Seeds short-tailed, the embryo 1–1.5 mm. long, the tail one third or one half as long.

CHINA: Kansu: (T'ao River basin) Choni, *J. F. Rock* 12587 (TYPE, A), 14926 (A, NY); same locality, W'm. Purdom 1021 (A); Toyüku, *J. F. Rock*

12821 (A, US); bank of T'ao, Tebbu, *J. F. Rock* 12870 (A, NY), 12883 (A, NY), 12873 (A, US); Ta-tsu-to, Kadjaku Valley, *J. F. Rock* 13603 (A); Poyuku, *J. F. Rock* 13659 (A), 13687 (A); Lien-hoa Shan, *J. F. Rock* 12749 (A); Lower Tebbu, Wan-tsang, *J. F. Rock* 14684 (A), 14813 (A), 14852 (A), 15046 (A, US); Mayaku near Nyipa Village, *J. F. Rock* 14791 (A, US), 15076 (A); Pezhu, *J. F. Rock* 14948 (A); Upper Tebbu, Ping-fan, *R. C. Ching* 484 (A, US); Li-chen, *R. C. Ching* 325 (A, US), 393 (A, US), 400 (A), 440 (US); Tien-schiu, in via Min-Schemo-Weitseba, *G. Fenzel* 2776 (A).

CULTIVATED: Arnold Arboretum 21675 (Rock seed no. 13603), *E. J. Palmer*, June 11, 1926 (A); *S. Y. Hu*, June 13, 1951 (A); Arnold Arboretum 21701 (Rock seed no. 14948); *E. J. Palmer*, July 6, 1937 (A).

Philadelphus kansuensis is known only from Kansu Province. The type was collected at Choni, where it occurs in forests along the banks of streams at altitudes of 2890 meters. The plant has been recorded as growing on the outskirts of *Picea* and *Abies* forests, mixed with *Juniperus* at altitudes of 2240 to 3050 meters. It is a shrub up to seven meters high, and its white fragrant flowers appear in July. *Rock* 14813 was collected in September and was still in flower.

Rehder interpreted this taxon as a variety of *P. pekinensis* Rupr. because of its general appearance, which resembles that of the latter species. This resemblance is rather superficial. The erect pubescence on the upper surface of the leaves, the villose stems, and the setose rim of the disc are not found in *P. pekinensis*. They suggest a closer relationship with *P. subcanus* Koehne. The hairs on the hypanthium are strigose-villose, resembling *P. sericanthus* Koehne. Thus morphologically *P. kansuensis* represents an ensemble of the traits of *P. pekinensis*, *P. subcanus*, and *P. sericanthus*. Geographically its range illustrates a very interesting principle for the understanding of the phytogeography of China. This species occurs only in southern Kansu, at the northern portion of Min-shan, which constitutes the western end of the Tsingling Range. At that place not only do the tributaries of the Yellow River have their source, flowing to the north, and those of the Yangtze River originate and flow to the south, but the point is also the junction of the mountains that constitute the backbones of northwestern, western, and central China. Northeastward from Min-shan runs the Tai-hang-shan Range, on which occurs *P. pekinensis*. Eastward is the Tsingling proper, where *P. sericanthus* occurs. Southeastward runs the north-south line of the Szechuan Alps, where *P. subcanus* is found. Thus the western portion of Tsingling, the Min-shan, forms a bridge to join the floras characteristic of North and West China. *Philadelphus kansuensis* certainly proves this.

Rock in 1926 sent seed lot 13603 to the Arnold Arboretum, and the seeds germinated in September 1929. The cultivated plants go under the number 13603. His seed lot 14948 reached the Arnold Arboretum in 1927. The Arboretum number of the plants raised from these seeds is 21701.

45. *Philadelphus schrenkii* Rupr. in Bull. Phys.-Math. Acad. Sci. St. Pétersb. 15: 365. 1857; et in Mél. Biol. 2: 542. 1858. — Koehne,

Deutsche Dendr. 182. 1893; in Gartenfl. 45: 596. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 84. 1904.—Komarov in Act. Hort. Petrop. 22: 429. 1903.—Maxim. Prim. Fl. Amur. 109. 1859.—Schneider, Ill. Handb. Laubh. 1: 372, fig. 237, *w-w²*. 1905.—Smith in Jour. Linn. Soc. Bot. 36: 500. 1905.—Nakai, Chosen Shokubutsu 1: 336, fig. 414. 1914; in Bot. Mag. Tokyo 29: 65. 1915; et Fl. Sylv. Kor. 15: 53, *pl. 12*. 1926.—Nekrasowa Fl. As. Russ. I. 3: 8. 1924.—Minami, List Pl. Manch. Mong. 183. 1926.—Rehder, Man. Cult. Trees Shrubs 276. 1927; ed. 2, 271. 1940; et Bibl. Cult. Trees Shrubs 193. 1949.—Poiarkova in Komarov, Fl. SSSR 9: 222. 1939.—Makino & Tanaka, Man. Fl. Nipp. 229. 1927.—Murakoski, Dai-zukan 7: 23. 1935.—Chen, Ill. Man. Chin. Trees Shrubs 374. 1937.—Kitagawa, Lineam. Fl. Mansh. 253. 1939.—Sato, Ill. Manch. Mong. Trees ed. 2, 129, fig. 91. 1943.—Bean, Trees Shrubs ed. 7, 2: 419. 1950; et in Chitt. Dict. Gard. 3: 1546. 1951.

Philadelphus coronarius Linn. γ *satsumi* Maxim. in Mém. Acad. Sci. St. Pétersb. Sér. VII. 10 (16): 40 (Rev. Hydrang. As. Or.). 1867, pro parte.

Philadelphus satzumi var. *schrenkii* Lavallée, Arb. Segrez. Enum. 115. 1877, *nom. nud.*

Philadelphus schrenkii f. *canescens* Komarov in Bull. Jard. Bot. Russe 16: 173. 1916.

Philadelphus tenuifolius var. *schrenkii* Vassiljev in Not. System. 8 (12): 219. 1940.

Philadelphus schrenkii f. *longipedicellatus* Nakai in Jour. Jap. Bot. 19: 374. 1943.

TYPE: Schrenk, Amur River.

An upright shrub 2–4 m. high, bark of two-year-old twigs gray, closed, smooth and longitudinally rimulose, rarely brownish gray with transverse cracks and tardily exfoliate, the current year's growth hirsute often becoming glabrescent, the hairs compressed. Leaves ovate, rarely ovate-elliptic, those on the vegetative shoot 7–13 cm. long, 4–7 cm. wide, those on the flowering shoot 4.5–7.5 cm. long, 1.5–4 cm. wide, obtuse or acute at the base, acuminate at the apex, remotely denticulate or subentire, very sparsely villose on the primary nerves beneath, glabrous or rarely sparsely pilose above. Flowers very fragrant, 5 or 7 (rarely 3) in a determinate raceme; the pedicels 6–13 mm. long, densely villose; hypanthium pilose, the sepals ovate, 4–7 mm. long, glabrous or glabrescent; corolla 2.5–3.5, very rarely up to 4 cm. across, the petals oblong-obovate, 1.5–1.8 cm. long, 1–1.2 cm. wide; stamens 25 up to 30; style half or more divided, hirtellous, the disk glabrous, the stigmata clavate, the abaxial stigmatic surface half the length of or subequal to the adaxial surface, and broader than the latter. Capsules ellipsoid, pointed at the apex, 6–9 mm. long, 4–5 mm. in diameter, the persistent sepals supermedian. Seeds short-tailed.

ASIA: Eastern Siberia and Manchuria: Er Tieng Tse, P. H. & J. H. Dorsett 3059 (US); Amur, S. Korshinsky in 1891 (US); C. S.

Sargent, Aug. 22, 1903 (A); B. V. Skvortzov, June 21, 1938 (A); R. Maak 43 (G), Maximowicz (G). Korea: K. S. Gilbert 32 (A), 46 (A), 59 (A); Pyengyang, R. K. Smith, May 12, 1934 (A); N. Kankyo, E. H. Wilson 8921 (A); Kogen, E. H. Wilson 10430 (US), 10514 (A, US); N. Heian, E. H. Wilson 10682 (A); Chiisan, Keisyonando, K. Uno 23252 (A).

CULTIVATED: United States: Arnold Arboretum, without collector, June 15, 1881, plant from St. Petersburg (A); 1047-37. S. Y. Hu, May 24, 1951 (A); 19356. S. Y. Hu, June 14, 1951 (A); State College, Pa., R. P. Meahl, June 1937; U. S. Dept. Agric. 72411, seeds obtained by P. H. Dorsett, collected in the Forest Concession of the Chinese Eastern Railway in the vicinity of Shitoukhetsy by I. V. Kosloff, Harbin (A).

Because of its hairy style *P. schrenkii* has created little confusion in botanical literature. Maximowicz interpreted it as being conspecific with the Japanese *P. satsumi* and placed them both in a variety of *P. coronarius*. In this he erred, for the Japanese taxon has a more or less glabrous hypanthium, and when hairs are present they are short and curly. Poiarkova in Komarov's Fl. SSSR. suggested that *P. schrenkii* has larger and more fragrant flowers than *P. tenuifolius*. Vassiljev took this suggestion and actually made the trinomial *P. tenuifolius* var. *schrenkii*, limiting it to plants producing flowers 3.5-4 cm. in diameter. As the size of the flower in all the species of *Philadelphus* varies considerably in relation to the vigor of the plant, the age of certain shoots, environmental conditions, and even the position of the individual flowers, flower size alone should not be used to delimit taxa. Our material seems to indicate that flowers 3.5-4 cm. in diameter are extremes rather than means. Thus U. S. Dept. Agric. 72411 bears flowers 3-4 cm. in diameter in Maryland, 2.5 cm. in Pennsylvania, and even smaller in California. Most of the flowers of the Maryland-grown plant are between 3 and 3.5 cm. in diameter, and only a few located in the center of the inflorescences are up to 4 cm. in diameter. Although the flower sizes in various plants of this number differ, their appearance, the shape of the petals, the indumentum on the pedicels and hypanthium as well as the hairs of the style are the same. In material from feral plants examined the condition is the same. I therefore cannot accept Vassiljev's conclusion. The pubescent style of *P. schrenkii* is a constant character. There is no indication that this character is a non-inheritable modification. Until our knowledge of the cytology of the closely allied species is fully understood, it is best to retain it as a distinct species.

Philadelphus schrenkii is closely related to *P. tenuifolius*. In other than the hairy style character of the former, there is little difference between them, either geographically or morphologically. The fruit shape and the position of the persistent calyx seem to provide some concomitant distinguishing characters. In *P. schrenkii* the fruits are ellipsoid, attenuate at both ends, with the calyx attached two thirds towards the distal end, while in *P. tenuifolius* the fruits are obconical, rounded at the distal end, the calyx nearly apical.

The natural range of distribution of *P. schrenkii* is eastern Siberia, Manchuria, and Korea. There it is a shrub about two meters high, common or

even abundant at altitudes from sea level to 1500 meters elevation. It flowers in late June and early July. Makino and Tanaka reported it as occurring in Japan, but it is suspected that it may have been introduced there.

45a. *Philadelphus schrenkii* var. *jackii* Koehne in Fedde, Rep. Spec. Nov. 10: 127. 1911.—Rehder, Man. Cult. Trees Shrubs 277. 1927; ed. 2, 271. 1940; et Bibl. Cult. Trees Shrubs 193. 1949.—Chen, Ill. Man. Chin. Trees Shrubs 374. 1937.—Bean in Chitt. Dict. Gard. 3: 1546. 1951.

Philadelphus lasiogynus Nakai in Bot. Mag. Tokyo 29: 67. 1915.

Philadelphus schrenkii sensu Nakai in Bot. Mag. Tokyo 29: 65. 1915, non Rupr. 1857.

Leaves on the flowering twigs ovate-elliptic, rarely ovate, 3.5–7 cm. long, 1.5–3.5 cm. wide, very sparsely pilose on both surfaces, especially on the primary nerves beneath, or glabrescent, remotely serrate, acute or obtuse at the base, shortly acuminate at the apex; flowers very fragrant, 5–7 in a raceme, the corolla 2.5–3.5 cm. in diameter, the petals oblong-obovate, 1–1.5 cm. long, 0.7–1 cm. wide, the stamens 25–35, the styles pubescent, the disk ± pubescent.

MANCHURIA: Kirin, F. H. Chen 407 (A); B. A. Irashkerich 427 (A); Shitokheza, D. Litvitvinov 2058 (A), 2852 (A); Swuifenco, B. V. Skwortzov on June 10, 1925 (A); Sieho, B. V. Skwortzov on Aug. 1, 1925; V. Komarov 833, 834 (A).

KOREA: N. Heian, French Mine, E. H. Wilson 8638A (A); N. Kankyo, Tumen-Yalu divide, E. H. Wilson 9075 (A); Hohari, Furumi, July 1, 1917 (A).

CULTIVATED: Arnold Arboretum 6595, from seed collected in Korea by J. G. Jack in 1905, A. Rehder, June 4, 1910 (TYPE, A), May 30, 1911 (A), June 3, 1912 (A); S. Y. Hu, June 14, 1951 (A); 423–39, grown from seed received from the Acad. Sci. USSR., S. Y. Hu, June 14, 1951 (A); Hort. H. H. Hunnewell, Wellesley, A. Rehder, June 14, 1899 (A).

The original species was dedicated to A. G. von Schrenk. Koehne in publishing the variety used the erroneous spelling *schrenckii*, and Nakai, who probably did not check the original publication, followed him.

The variety was based on a plant cultivated in the Arnold Arboretum. The characters that Koehne emphasized hold for the cultivated plants after more than forty years. Although specimens collected in 1951 have smaller and fewer flowers, the indumentum, the style and the disk are identical with those of specimens collected in 1910. Specimens from feral plants that possess a hairy disk seem to be more or less glabrous. In this respect they more closely resemble typical *P. schrenkii* than *P. schrenkii* var. *jackii*. These specimens also exhibit a gradual change in the density of the disk pubescence from barely evident to partially pubescent to rather densely pubescent. Apparently the disk indumentum is variable. Nakai, without examining Koehne's type, treated *P. schrenkii* var. *jackii* as a synonym of *P. schrenkii*, and described the Korean *P. lasiogynus* as

a new species, characterized by having a pubescent disk. I see no reason for distinguishing this from Koehne's variety.

In the living *Philadelphus* collection at the Arnold Arboretum, no. 423-39 is a species under an apparently unpublished binomial, the species being dedicated to Rafinesque. This was raised from seeds obtained from the Academy of Science, U.S.S.R. But it is typical *P. schrenkii* var. *jackii* in all respects, even to the hairs on the lower surface of the leaves. At the Arnold Arboretum it flowers in mid-June. The flowers are white and fragrant, with the petals narrowly tinged red on the back along the median line, and the sepals are pale yellowish green.

45b. *Philadelphus schrenkii* var. *mandshuricus* (Maxim.) Kitagawa, Lineam. Fl. Mansh. 253. 1939.

Philadelphus coronarius var. *mandshuricus* Maxim. in Mém. Acad. Sci. St. Pétersb. Ser. VII. 10 (16): 41 (Rev. Hydrang. As. Or.). 1867.

Philadelphus mandshuricus (Maxim.) Nakai in Bot. Mag. Tokyo 29: 66. 1915. — Nekrasowa, Fl. As. Russ. I. 3: 7. 1924, as "manshuricus."

Philadelphus amurensis Komarov in Bull. Jard. Bot. Russe 16: 170. 1916.

Philadelphus schrenkii sensu Rehder, Man. Cult. Trees Shrubs 277. 1927; ed. 2, 271. 1940; et Bibl. Cult. Trees Shrubs 193. 1949, pro parte, in syn., non Ruprecht.

Leaves broadly ovate, up to 8 cm. long, 5 cm. wide, rounded or obtuse at the base, the apex shortly acuminate, the margin finely but remotely serrate; flowers 5 or 7, 3-3.5 cm. in diameter, the hypanthium sparsely hirsute, the petals suborbicular, 1.2-1.5 cm. in diameter, the style pubescent, the disk \pm pubescent.

MANCHURIA: Mandshuria austro-orientalis, St. Olga, *Maximowicz*, June 21, 1860 (ISOTYPE of *P. coronarius* var. *mandshuricus* Maxim., G, US).

CULTIVATED: Arnold Arboretum 534 under an unpublished trinomial.

Maximowicz characterized this as having large, inodorous or disagreeably odorous flowers, its petals subrotundate. Nakai treated this taxon as a species but gave no reason for this; his concept was adopted by Nekrasowa. Judging from their keys, both assumed the plant to have a glabrous style, and they overlooked the petal characters that Maximowicz employed to distinguish the variety. With an isotype before me, I believe that Kitagawa was correct in transferring it to *P. schrenkii* as a variety.

46. *Philadelphus hupehensis* (Koehne), stat. nov.

Philadelphus ineanus var. *sargentianus* forma *hupehensis* Koehne in Fedde, Repert. Sp. Nov. 10: 127. 1911; et in Sarg., Pl. Wils. 1: 145. 1912.

TYPE: *E. H. Wilson*, Veitch Exp. 833 (A).

A shrub, the branches gray, the bark of the second year's growth closed, longitudinally rimulose, the current year's growth villose. Leaves elliptic, 7-10 cm. long, 2.5-5 cm. wide, acute, rarely obtuse at the base, acuminate

at the apex, sharp-serrate, uniformly hirsute above, the hair erect, compressed at the base, sparsely strigose on the principal nerves and veinlets beneath. Inflorescence 9-, 13-, 19-, or 7-flowered; pedicels dense-strigose and incanous, the lower pairs sometimes branched, each carrying a cyme of 3 flowers; hypanthium and calyx strigose, more or less incanous, the sepals ovate, 6 mm. long, 3 mm. wide at the base; corolla disciform, 1.5-2 cm. across, the petals obovate-suborbicular, 10 mm. in diameter, sparsely pilose at the base of the back; stamens ca. 35, disc and style pilose, the pubescence straight; the style 4 mm. long, undivided, the stigmata spatulate. Capsules subglobose-ovoid, 9 mm. long, 8 mm. in diameter, the persistent sepals subapical. Seed short- or medium-caudate, the embryo 1.25 mm. long, the tail half as long, the testa brown.

CHINA: Hu pei: Fang Hsien, *E. H. Wilson* 581 (A, G); without precise locality, possibly Ichang, *E. H. Wilson*, Veitch Exp. 833 (A, TYPE); Wan-tsao Shan, *W. Y. Chun* 3918 (A). Shensi: Kiu San, *Jos. Giraldi* in 1897 (A); Kiu-gua San, *Jos. Giraldi*, July 10, 1897 (A). Yunnan: Suen-oui, *E. E. Maire* 403 (A); Yong-shan Hsien, *H. T. Tsai* 51182 (A).

The density of the hairs on the lower leaf surface of this species indicates an intermediate position between *P. incanus* and *P. sericanthus*. The erect hairs on the upper surface of the leaves and the white indumentum on the hypanthium suggest a closer relationship with *P. incanus* than with *P. sericanthus*. On the strength of these characters Koehne was right in placing it as a variety of the former species. Nevertheless, he overlooked the presence of hairs on the style, a character never found in *P. incanus*. Within this series *P. subcanus* and *P. schrenkii* are the species that have pubescent styles. The type of the indumentum and the total appearance of this species are different from those characters in *P. subcanus*. *Philadelphus schrenkii* is a species from Manchuria and Korea. Besides the morphological differences that exist between the present species and *P. schrenkii*, there is also the geographical separation. After considering every possible alliance, I find it necessary to raise the status of this taxon from that given it by Koehne.

Series 8. *Satsumani* (Koehne), stat. nov.

Philadelphus subg. II. *Euphiladelphus* sect. 4. *Stenostigma* ser. 8. *Satsumani* (Koehne), stat. nov.

Philadelphus sect. *Stenostigma* subsect. *Satsumani* Koehne in *Gartenfl.* **45**: 450. 1896; et in *Mitt. Deutsch. Dendr. Ges.* **1904** (13): 82, 84. 1904.

Philadelphus sect. *Satsumani* (Koehne) Nakai in *Bot. Mag. Tokyo* **29**: 64. 1915; et in *Jour. Jap. Bot.* **19**: 371. 1943.

Philadelphus sect. *Coronarii* (Koehne) Nakai, l.c., pro parte.

Philadelphus ser. *Coronarii* (Koehne) Rehder, *Man. Cult. Trees Shrubs* ed. 2, 269. 1940; et *Bibl. Cult. Trees Shrubs* 192. 1949, pro parte.

TYPE SPECIES: *P. satsumanus* Sieb. ex Miq.

Medium-sized upright shrubs, the bark closed; leaves ovate or ovate-

elliptic, caudate or acuminate at the apex; inflorescences 7-, 5-, rarely 3-flowered, the hypanthium sparsely pubescent or only on the angles, the hairs golden, curly; corollas generally small, 2–3 cm. across; stamens 23–30; abaxial stigmatic surface broad, equal to or half the length of the adaxial surface; capsules ovoid or ellipsoid; seeds medium-caudate.

KEY TO THE SPECIES

- A. Style glabrous.
- B. Leaves uniformly pubescent 47. *P. satsumanus*.
- BB. Leaves glabrous except on the primary nerves and in their angles beneath. 48. *P. satsumi*.
- AA. Style pubescent; leaves glabrous above, glabrous except the primary nerves and their angles beneath. 49. *P. shikokianus*.

47. ***Philadelphus satsumanus* Sieb. ex Miq. in Ann. Mus. Bot. Lugd.-Bat. 3: 99. 1867.** — Rehder in Mitt. Deutsch. Dendr. Ges. 1910 (19): 249. 1910; Man. Cult. Trees Shrubs 275. 1927; ed. 2, 269. 1940; et Bibl. Cult. Trees Shrubs 192. 1949, pro parte. — Engler, Pflanzenf. ed. 2, 18a: 194. 1930, pro parte.

Philadelphus coronarius var. *satsumanus* Jäger, Zierzchöltz ed. 2. 236. 1884.

Philadelphus matsumuranus Koehne in Gartenfl. 45: 619. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 86. 1904. — Schneider, Ill. Handb. Laubh. 1: 374. 1905. — Makino & Tanaka, Man. Fl. Nipp. 228. 1927.

Philadelphus satsumanus var. *nikoensis* Rehd. in Mitt. Deutsch. Dendr. Ges. 1910 (19): 249. 1910; Man. Cult. Trees Shrubs 275. 1927; ed. 2, 269. 1940; et Bibl. Cult. Trees Shrubs 192. 1940.

Philadelphus satsumi sensu Nakai in Bot. Mag. Tokyo 29: 64. 1915, pro parte, non Sieb. ex Lindl. & Paxt.

Philadelphus gordonianus var. *parviflorus* Dippel, Handb. Laubh. 3: 343. 1893.

Philadelphus yokohama Dippel, l.c., non Lavallée, 1877.

Philadelphus satsumi var. *yokohama* Dippel, l.c., in syn.

TYPE: *Siebold* (Mus. Bot. Lugd.-Bat., Leyden).

An upright shrub 1.5–2.5 m. high, bark of the two-year-old twigs castaneous, closed, longitudinally rimous, rarely brown and tardily exfoliate; current year's growth pubescent or glabrescent. Leaves uniformly and sparsely pilose above, tomentose beneath; those on the vegetative shoots ovate, rarely ovate-elliptic, 5–10 cm. long, 2.5–6 cm. wide, rounded, rarely obtuse at the base, caudate, rarely acuminate at the apex; those on the flowering shoots ovate, rarely elliptic, 3–7 cm. long, 1–3.5 cm. wide, obtuse, rarely rounded at the base, acuminate at the apex, remotely and finely serrate. Flowers 5 or 7 in a raceme, the lower pairs in the axils of normal leaves; the pedicels 4–6 mm. long, pilose, the hypanthium pilose along the nerves or all over; sepals ovate, 4 mm. long, often pilose; corolla 2.5–3 cm. across, rarely smaller, the petals oblong-ovate, 1–1.4 cm. long, 0.7–1 cm. wide; stamens 25–30; styles glabrous, entire or slightly divided, the adaxial stigmatic surface equal to or slightly shorter than the

abaxial. Capsule obovoid, the persistent sepals attached one fourth below the apex. Seeds medium-caudate.

JAPAN: Hon do: Asama, *U. Faurie* 6264 (A); Shinano, *J. G. Jack*, Sept. 3, 1905 (A); same locality, *S. Okuyama* on July 2, 1949 (BH, fragment in A); Musashi, U. S. Dept. Agric., May 19, 1911 (US); same locality, *M. Mizushima* 2020 (A), 2587 (A); Kai Kofu, *K. Sakurai*, June 9, 1910 (A); Nikko, *N. Mochizuki*, Aug. 30, 1909 (A, G); same locality, *J. A. Veitch*, Oct. 18, 1892 (A, TYPE of *P. satsumanus* var. *nikoensis* Rehder); Mino, *K. Shiota* 1326 (A), 8919 (A); Ontakesan, *G. Koizumi*, Aug. 1910 (BH); Uraminotaki, *T. Sawada* 2194 (A); Tokyo, *S. Suzuki* 289 (A); Mt. Ominein Yamato, *H. Tanaka*, July 17, 1933 (C); Nitromine-san, *E. H. Wilson* 6964 (A); Utake-gawa, *E. H. Wilson* 9661 (A, US); Kozuke, *M. Mizushima* 1267 (A), 1869 (A); Shimotsuke, *M. Mizushima* 2124 (A), 2299 (A), 2351 (A).

CULTIVATED: Europe: Germany: Hort. Götting, *A. Rehder*, July 1, 1890 (A). Austria: *H. Braun*, June 18, 1907 (A). United States: Arnold Arboretum 1580-4, without collector, Sept. 21, 1897 (A), June 19, 1899 (A); 5097, without collector, June 13, 1914 (A), June 21, 1916 (A).

Both morphologically and ecologically this species is very closely allied to *P. satsumi* Sieb. ex Lindl. & Paxt., yet the tomentose lower leaf surface is distinctive. In general the hypanthia of this species are more pubescent than those of *P. satsumi*. Nevertheless, there seems to be much variation in the density of the pubescence on the hypanthia of this species. A few of the specimens that I have examined even have subglabrous ones.

48. *Philadelphus satsumi* Sieb. ex Lindl. & Paxt. in Fl. Gard. 2: 102, fig. 188. 1852. — Koch, Dendr. 1: 338. 1869. — Nicholson, Ill. Dict. Gard. 3: 95. 1886. — Koehne, Deutsche Dendr. 180. 1893; in Gartenfl. 45: 562. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904 (13): 84. 1904. — Schneider, Ill. Handb. Laubh. 1: 371, fig. 237, f-h. 1905. — Nemato, Nippon Shokubutsu soran hoi (Fl. Jap. Suppl.) 295. 1936. — Makino, Ill. Fl. Nipp. 487, fig. 1461. 1940.

Philadelphus coronarius var. *satsumi* Maxim. in Mém. Acad. Sci. St. Pétersb. Sér. VII 10 (16): 40 (Rev. Hydrang. As. Or.) 1867, excl. syn. — Dippel, Handb. Laubh. 3: 337. 1893. — Makino & Tanaka, Man. Fl. Nipp. 228. 1927. — Makino & Nemato, Nippon Shokubutsu soran 443. 1933. — Terasaki, Nippon Shokubutsu zufu, pl. 388. 1933. — Murakoshi, Dai-zukan 7: 23, fig. 47. 1935. — Kia, Pl. Sin. Ill. 702, fig. 1217. 1937.

Philadelphus chinensis Hort. ex Koch, Dendr. 1: 339. 1869. — Nicholson, Ill. Dict. Gard. 3: 95. 1886.

Philadelphus satsumanus sensu Koch, Dendr. 1: 339. 1869. — sensu Rehder in Mitt. Deutsch. Dendr. Ges. 1910 (19): 249. 1910; Man. Cult. Trees Shrubs 275. 1927; ed. 2, 269. 1940; et Bibl. Cult. Trees Shrubs 192. 1949. — sensu Bean, Trees Shrubs ed. 7, 2: 419. 1950, non Sieb. ex Miq. 1867.

Philadelphus nepalensis Hort. ex Koch, Dendr. 1: 339. 1869.

Philadelphus roylei Hort. ex Koch, l.c. — Nicholson, Kew Hand-list 1: 227. 1894, 377. 1902.

Philadelphus speciosus sensu Koch, l.c. — Nicholson, l.c., non Schrader, 1828.

Philadelphus ledebourii Hort. ex Koch, l.c. — Nicholson, l.c.

Philadelphus pekinensis sensu Koch, l.c., non Rupr. 1857.

Philadelphus schrenkii sensu Maxim. in Mém. Acad. Sci. St. Pétersb. Sér. VII. 10 (16): 40 (Rev. Hydrang. As. Or.) 1867, pro parte. — sensu Koch, l.c., pro parte, non Rupr. 1857.

Deutzia japonica Hort. ex Koch, l.c. — Nicholson, l.c.

Deutzia pulchella Hort. ex Koch, l.c. — Nicholson, l.c.

Deutzia undulata Hort. ex Koch, l.c.

Deutzia sanguinea Hort. ex Koch, l.c.

Deutzia gracilis Hort. ex Koch, l.c., non Sieb. & Zucc. 1835.

Deutzia thyrsiflora Hort. ex Koch, l.c.

Deutzia corymbosa Hort. ex Koch, l.c., non R. Brown, 1835.

Philadelphus acuminatus Lange in Fortegn. Veter.-Landboh. Frilandstr. 65. 1871; et in Bot. Tidskr. III. 2: 131, pl. 2. 1878. — Schneider, Ill. Handb. Laubh. 1: 371. 1905.

Philadelphus japonicus Hort. ex Nicholson, Kew Hand-list 1: 227. 1894; et ed. 2, 377. 1902.

Philadelphus pulchellus Hort. ex Nicholson, ll.cc.

Philadelphus coronarius var. *acuminatus* (Lange) A. H. Moore in Rhodora 17: 122. 1915.

Philadelphus satsumi var. *nikoensis* Nemato, Nippon Shokubutsu soran hoi (Fl. Jap. Suppl.) 295. 1936.

TYPE: Siebold (Roy. Hort. Soc. Gard., Wisley).

An upright shrub 1.5–3 m. high, the bark of the two-year-old twigs brown, closed and longitudinally rimulose, tardily exfoliate; current year's growth slender, glabrescent. Leaves very sparsely setose or glabrous above, hirsute on the primary nerves and bearded in their angles beneath; those on the vegetative shoots ovate or broadly elliptic, 6–9 cm. long, 3–5 cm. wide, remotely and coarsely serrate, obtuse or rarely rounded at the base, acuminate or caudate at the apex, the acumen up to 2 cm. long; those on the flowering twigs ovate or ovate-lanceolate, 4.5–7 cm. long, 1.5–4.5 cm. wide, acute or obtuse or very rarely rounded at the base, acuminate or caudate at the apex. Flowers slightly fragrant, 5 or 7 in a raceme, rarely 2 or 3 terminating the branchlet, the pedicels 6–8 mm. long, pilose; hypanthium pilose at the angles or on the nerves, otherwise glabrous, the hairs short, curly, and golden, the sepals ovate, 6 mm. long; corolla 3 cm. across, the petals oblong-ovate or ovate, 1.3–1.5 cm. long, 0.9–1 cm. wide; stamens 30; style glabrous, shortly divided at the apical end, the abaxial stigmatic surface equal to or slightly shorter than and twice as broad as the adaxial surface. Capsules ellipsoid, attenuated at both ends, more so at the base. Seeds medium-caudate.

JAPAN: Near Shojiko, Fujiyama region, *P. H. Dorsett & W. J. Morse* 383 (US); Musashi, *H. Ito* 190 (BH); Shinano, *J. G. Jack*, Sept. 4, 1905 (A); same locality, *M. Mizushima* 2223 (A); Hida, *K. Shiota* 6741 (A); Senano, *Tschonoski* in 1864 (G, US); Nambu, *Tschonoski* in 1865 (G, US); Idzu, *Tschonoski* in

1866 (US); Nanokawa, Tosa, *K. Walanabe*, June 14, 1889 (G); Hayachima-san, *E. H. Wilson* 7563 (A); Hakone, *E. H. Wilson* 10364 (A); Naganoken, *K. Uno*, Aug. 28, 1951 (A); Kanagaloa, *S. Suzuki*, June 4, 1951 (A).

CULTIVATED: Europe: Kew, *G. Nicholson*, June 16, 1880 (A), Sept. 28, 1882 (A); *Macklean* 381 (B); Hort. Bot. Berol., *E. Koehne* 363 (A, G); Hort. Späth, *C. Schneider*, June 27, 1902 (A); Hort. Götting, *A. Rehder*, July 1, 1890 (A), June 17, 1894 (A). United States: Arnold Arboretum 15414 (A).

Among the earlier known species of *Philadelphus* this one has caused the most confusion in botanical literature. To clarify the confusion, the following data must be considered: (1) *Philadelphus satsumi* Sieb. ex Lindl. & Paxt. was the first binomial assigned to this Japanese *Philadelphus*. (2) Siebold, as a result of his voyage to Japan, introduced living specimens to Europe and provided Zuccarini with herbarium material. Both living and dry material had reached Lindley and Paxton before 1852, when they prepared a very inadequate illustration and description of *P. satsumi* Sieb. The flowering branches of their living material, from which the illustration was made, bore only two or three flowers. Yet they compared their living form with a Japanese specimen provided by Professor Zuccarini. Consequently, regarding the number of flowers of the species they remarked, "They . . . appear hereafter in long interrupted racemes with linear or almost filiform bracts. The calyx is smooth." As to the leaves, they stated that the foliage was slightly hairy on the under side, the lower leaves ovate-lanceolate, acuminate, and with a few shallow very acute serratures. (3) The Siebold Company published a nursery catalogue in 1856, in which, on page 337, *P. satsumanus* appeared as a *nomen nudum*. (4) Miquel in 1867 described this catalogue entry, *P. satsumanus* Sieb., as having its calyx tube densely pubescent, and its broadly ovate or elliptic leaves sparsely puberulent above and on the reticulations beneath. (5) Koch in 1869 extended the range of the species to China and the Himalayan region and thus created many synonyms. (6) Maximowicz in 1867 considered the Japanese species identical with *P. schrenkii* of Manchuria and combined them, making a variety of *P. coronarius*. (7) Koehne in 1893 interpreted *P. satsumi* Sieb. ex Lindl. & Paxt. as conspecific with *P. laxus* Schrader and redescribed *P. satsumi* on the basis of a specimen cultivated in the Berlin Botanical Garden. He characterized it as having a glabrous hypanthium and calyx, or only the hypanthium somewhat hairy; the lower surface of the leaves glabrous or only slightly hairy on the reticulations; and the raceme with seven flowers. (8) Rehder in 1910, 1927, 1940 and 1949 accepted Koehne's concept of the species. As he considered *P. satsumi* Siebold a preoccupied name, he adopted Miquel's binomial for the form described by Koehne and ascribed to *P. satsumanus* var. *nikoensis* the form represented by the Japanese *Philadelphus* having its leaves pubescent beneath. (9) Nemato reduced Rehder's variety to *P. satsumi* Sieb. ex Lindl. & Paxt. and accidentally published the trinomial *P. satsumi* var. *nikoensis* Nemato.

The feral Japanese material that I have examined contains two distinct

elements, one with an almost glabrous hypanthium, pubescent with short curly golden hairs only at the base or on the angles. The leaves of this element are usually glabrous beneath except on the primary nerves and in their axils. The other element has a uniformly pubescent hypanthium and the lower leaf-surface is pubescent throughout. Specimens from cultivated plants at Kew, Berlin, and the Arnold Arboretum show both characters. It is most likely that in the Siebold introduction both elements were involved. What Lindley and Paxton described was the glabrous one, and what Miquel described was the more pubescent one.

A comparative study of the Japanese specimens and the continental forms, including collections cited by Maximowicz, indicates that several distinct species are represented. The Japanese species differs from the mainland forms in the short golden curly pubescence on the ridges or all over the hypanthium, in the broader and longer abaxial stigmatic surfaces, and in the medium or long-tailed seeds. Maximowicz' interpretation of the Japanese and Manchurian species as identical is not justified morphologically.

Lindley and Paxton worked in London. Specimens collected from plants cultivated at Kew 1880-1890 agree with the spontaneous Japanese specimens in the outline of the leaves, the indumentum, in the size of the flowers, the shape of the petals, the length and division of the styles, the width of the stigmatic surfaces, and the tails of the seeds. These specimens may represent descendants of the form that Lindley and Paxton described. In all respects they are identical with Koehne 363, the basis of the latter's description of *P. satsumi* Sieb. Thus specimens from plants cultivated in England and Germany prove the two taxa to represent one and the same species. The only character that might lead one to doubt the identity of Lindley and Paxton's species and that of Koehne is the number of flowers on a flowering twig, the former having two or three flowers, while in the latter the inflorescence is usually seven-flowered. But this difference occurs also in nature. Most of our Japanese material has five or seven flowers on a twig, but Jack's Shinano specimen bears only two or three flowers. In this case the material was collected from a very old plant. The flowering twigs are apparently developed from lateral accessory buds. Very likely Lindley and Paxton's living material was somewhat anomalous, as is often the case when a recently planted specimen first flowers. They did, however, explain that the herbarium specimen sent by Zuccarini had an inflorescence in the form of a long interrupted raceme. Miquel's description represents a distinct but closely related species with uniformly pubescent lower leaf surfaces.

Judging from Lange's description and illustration, his *P. acuminatus* is identical with *P. satsumi* Sieb. ex Lindl. & Paxt. A. H. Moore proposed *P. coronarius* var. *acuminatus* on the basis of *P. satsumi*. Naturally it becomes a synonym here.

In Japan *P. satsumi* occurs at altitudes between 600 and 1000 meters. It is common along the roadsides, in woods or thickets, especially on the lava beds.

Maximowicz in 1867 cited *Wilford* 1859 from Tsusima Island as belonging here. Koehne in 1896 and Engler in 1930 both recorded it from the same island. The Wilford material in the Gray Herbarium is definitely *P. tenuifolius* Rupr. ex Maxim. I have seen no spontaneous material other than that from Hondo of Japan.

49. *Philadelphus shikokianus* Nakai in Bot. Mag. Tokyo 29: 66. 1915.—Murakoshi, Dai-zukan 7: 23. 1935.—Nemato, Nipp. Shok. soran hoi (Fl: Jap. Suppl.) 295. 1936.

Philadelphus yokohama Sieb. ex Lavallée, Arb. Segrez. Enum. 115. 1877.—Nicholson, Kew Hand-list 1: 227. 1894, *nom. nud.*

Philadelphus sinensis Hort. ex Lavallée, Arb. Segrez. Enum. 115. 1877, *nom. nud.*

TYPE: *T. Makino*, June 14, 1889 (Japan).

An upright shrub, branchlets slender, bark of two-year-old twigs brown, closed or tardily exfoliate, the current year's growth 1–2 mm. in diameter, pubescent. Leaves glabrous or along the margin sparsely hirtellous above, glabrous beneath except on the nerves and in their angles; those on the vegetative shoots ovate or broadly elliptic, 8–10 cm. long, 3.5–6 cm. wide, acute or rounded at the base, caudate at the apex, remotely serrate; those on the flowering twigs lanceolate or ovate, 4–8 cm. long, 1.5–3.5 cm. wide, acute or rounded at the base, acuminate at the apex, remotely and finely serrate. Inflorescence 5- or 7- or rarely 9-flowered, the lowest pair in the axils of normal leaves, the pedicels 8–12 mm. long, pilose; hypanthium uniformly pubescent, the calyx lobes ovate, acuminate, pubescent, 4–7 mm. long; corolla 2–2.5 cm. across, the petals oblong, 8–12 mm. long, 6–8 mm. wide; stamens 19–23; disk and style pubescent, the style slightly divided, the abaxial stigmatic surface short and broad, half the length of the adaxial. Capsules obovoid, the persistent sepals attached one third below the apex. Seeds medium-caudate.

JAPAN: Shikoku: Tosa, Nanokawa, *K. Watanabe*, June 14, 1889 (G. TOPOTYPE); same locality, no collector, on June 21, 1891 (US. TOPOTYPE); Todigatayama, *K. Watanabe*, Aug. 11, 1888 (G). Hondo: Kobe, *K. Uno* 18965 (A), 18966 (BH); Mino, *K. Shiota* 6780 (A).

CULTIVATED: Europe: Kew, *G. Nicholson* 2595 (under the name *P. yokohama* Sieb.); Bot. Garten Forstakadamie, Hannover, *H. Zabel* (A). United States: Arnold Arboretum 9045, *C. E. Kobuski & C. K. Allen*, June 10, 1933 (A); Cambridge Bot. Gard., *R. Cameron*, June 18, 1918 (A).

This species is very closely related to *P. satsumi* Sieb. ex Lindl. and Paxt. Both of them have almost glabrous lower leaf surfaces, but *P. shikokianus* can readily be distinguished by its pubescent style.

Specimens collected at Kew by G. Nicholson in 1881 under the name *P. yokohama* Sieb. and by H. Zabel at Hannover, named *P. yokohamae* definitely belong here. They represent the *nomen nudum* Nicholson published in 1894.

(To be continued)

STUDIES ON THE PROGENY OF TRIPLOID PHILADELPHUS AND FORSYTHIA

DEXTER R. SAMPSON *

With one plate

THE ARNOLD ARBORETUM breeding program for horticultural plants, under the direction of Professor Karl Sax, has included the production of artificial tetraploids. By backcrossing the tetraploids to diploids outstanding *Forsythia* triploids have been produced. The next step has been to obtain aneuploid progeny from the triploids. The present report is concerned with aneuploid progenies of triploid *Philadelphus* and *Forsythia*.

PHILADELPHUS

Origin of the Triploid. Natural polyploidy within the genus *Philadelphus* has not yet been reported, all counts on pure species indicating $2n = 26$ (Bangham, 1929; Janaki Ammal, 1951). However in the progeny of the tri-species hybrid *P. purpureo-maculatus* triploids have occurred with $2n = 39$ (Janaki Ammal, 1951). These triploids, which are known as "Bicolore," "Belle Etoile" and "Sybille," are the finest *Philadelphus* cultivars yet to be produced. According to Janaki Ammal the parent diploid *P. purpureo-maculatus* is a hybrid between *P. lemoinei* and *P. coulteri* of Mexico, while *P. lemoinei* in turn is a hybrid between *P. coronarius* of Europe and *P. microphyllus* of southwestern U.S.A. Dr. Hu (1954) doubts that the rare *P. coulteri* was in fact one parent of *P. purpureo-maculatus*. At any rate, the genetic background of *P. "Bicolore,"* the triploid used in the present study, is complex.

Meiosis in the Triploid. Meiosis was studied in *P. "Bicolore"* to learn what chromosome numbers could be expected in the resulting gametes.

Analysis of twelve metaphase I plates showed 2 to 7 univalents with an average of 4.42, 2 to 11 bivalents with an average of 6.42, and 4 to 11 trivalents with an average of 6.92, while two cells showed one quadrivalent each, an average of 0.17. In one cell all but two chromosomes entered into pairing relationships, with two univalents, two bivalents and eleven trivalents being formed. This behavior is interpreted to mean there is a high degree of homology among the three chromosome sets of *P. "Bicolore."*

Anaphase I was characterized by the occurrence of lagging univalents while a few cells showed one or two bridges.

* The writer wishes to acknowledge his indebtedness to Professor Karl Sax who initiated the project, to Mr. Louis Lipp who cared for the plants, and to Dr. S. Y. Hu who provided valuable information on *Philadelphus*.

Similarly Anaphase II was characterized by lagging chromosomes and an occasional bridge. The manner in which the chromosomes were being distributed to the poles was determined by counting the number of chromosomes approaching one pole in each of sixty cells. Rarely could counts be made on more than one pole per cell. The results are given in TABLE I.

TABLE I. Distribution of Chromosomes at Anaphase II of *P. "Bicolore."*

Chromosome Number	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Observed Frequency	1	3	2	5	5	13	14	8	3	3	3	0	0	0
Expected Frequency					$\underbrace{3}_{3}$				$\underbrace{5}_{9}$				$\underbrace{5}_{3}$	

The mean chromosome number for the sixty counts was 18.46 ± 2.23 , which indicates a loss of 16% of the supernumerary chromosomes of the triploid. The frequencies expected if the thirteen extra chromosomes were distributed at random are given by the terms of the binomial $(0.5 + 0.5)^{13}$ taken to the nearest whole number. When the expected and observed frequencies are compared by chi-squared analysis, (classes 13–17 and 21–26 combined) the lack of fit is highly significant. $\chi^2 = 15.7$ and $P = < 0.01$ for four degrees of freedom.

At telophase II micronuclei were observed in a number of cells. These would account for all or part of the 16% loss of extra chromosomes.

The triploid Progeny. The triploid *P. "Bicolore"* sets few viable seed so that attempts to raise progeny from controlled pollinations were unsuccessful. However, by harvesting all the capsules which developed by open pollination, enough seed was obtained to start two sizable progenies.

The first progeny consisting of about 90 plants was started in the greenhouse early in 1951 but only 76 of these lived long enough to be set out in the field. By the summer of 1953 only 44 plants remained alive and their chromosome numbers were determined using iron-acetocarmine leaf squashes. The frequency of the different chromosome numbers is indicated in TABLE II and FIG. I.

The second progeny of *P. "Bicolore"* was started in the greenhouse in the spring of 1954 and all 44 of these plants survived the summer. Similarly their chromosome numbers were determined and the results are given in TABLE II and FIG. I.

TABLE II. Frequencies of different chromosome numbers in the two progenies of *P. "Bicolore."*

Chromosome Number	26	27	28	29	30	31	32	33	34	35	36	37
1951 Progeny	15	13	6	4	1	3	1	0	1	0	0	0
1954 Progeny	7	9	10	3	3	5	1	1	1	1	2	1
	22	22	16	7	4	8	2	1	2	1	2	1

It is evident that most individuals in both progenies have the diploid

or near diploid somatic chromosome number. This is vastly different from the distribution of chromosome numbers expected in zygotes formed by the random recombination of gametes having the chromosome numbers observed at anaphase II in *P. "Bicolore."* It is also greatly different from what would be expected if *P. "Bicolore"* were pollinated by a diploid (FIG. I). It appears that the higher aneuploid numbers are strongly se-

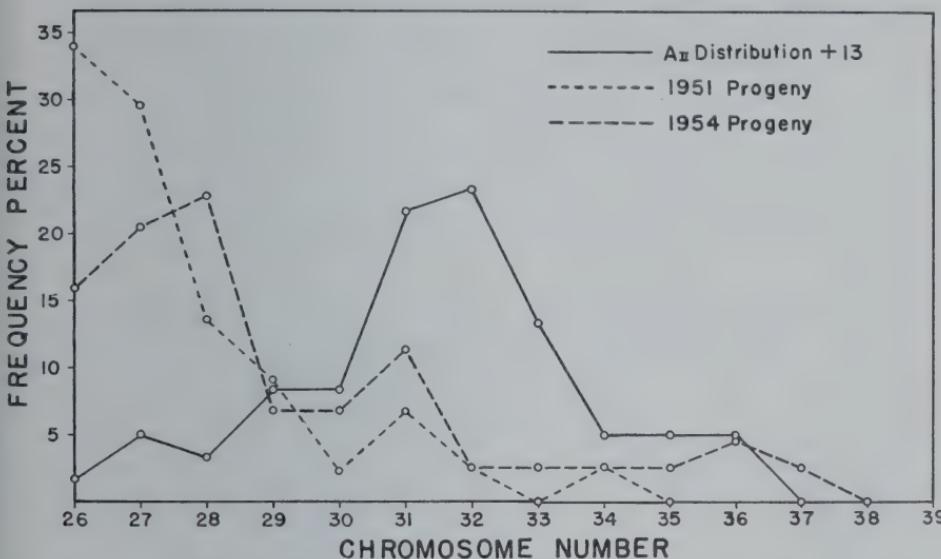


FIG. 1. Distribution of somatic chromosome numbers in the 1951 and 1954 *Philadelphus* progenies compared with the expected distribution if the triploid were pollinated by a diploid.

lected against at various stages leading to the development of seed for, although 46 per cent of the pollen of *P. "Bicolore"* appears morphologically good, only three to twenty percent of the ovules per capsule develop into full seeds. In addition, the difference between the 1951 and 1954 progenies in the chromosome number frequencies suggests that this selection against the higher aneuploids has continued well into the seedling stage. After the 1951 progeny had suffered over 50 per cent mortality its mean chromosome number was 27.6 ± 4.6 while the mean for the 1954 progeny, which had suffered less than one per cent mortality was 29.1 ± 5.3 . When the two distributions are compared by chi-squared analysis (classes 29-37 combined) the difference is found to be highly significant. $\chi^2 = 16$ and $P = < 0.01$ for three degrees of freedom.

Both progenies were distinguished by their enormous variability in habit, leaf shape, vigor and flower morphology. Representative leaf types are shown in Plate I together with the somatic chromosome number of the plant from which the leaf was taken. Only one leaf per plant is shown and as a rule it was taken from the middle of the largest branch. It is evident there is no correlation between leaf type and chromosome number.

To obtain a size index, and thus a vigor index, for each plant the lengths of all main stems and branches were measured and the measurements added together. In 1953 the size index for the plants of the 1951 progeny ranged from 28 to 1100 inches. The three smallest plants totaled 28, 29 and 44 inches and had 27, 28 and 26 chromosomes respectively. These three dwarfs are mentioned especially as they were the only members of the 1951 progeny which failed to survive the winter of 1953-54. At the end of the 1954 growing season the 41 survivors of the 1951 progeny ranged in size index from 120 to 3400 inches. The distribution of these plants according to size index and chromosome number is given in TABLE III. To determine whether or not there was any correlation between vigor and chromosome number the coefficient of correlation between size index and chromosome number was calculated for both years using ungrouped data. For the 1953 measurements $r = -.1288$ and for the 1954 measurements $r = -.1127$. In both cases r was not statistically significant.

TABLE III. Distribution of the 1954 survivors of the 1951 *Philadelphus* triploid progeny according to size index and chromosome number. (f) indicates one or more members of a particular class flowered in 1954.

Size Classes	Chromosome Numbers								Totals
	26	27	28	29	30	31	32	34	
100-200 ins.		1		1f			1		3
201-300	2	2	1						5
301-400	1			1		1			3
401-500	1f	4f	1f	2f		1			9
501-600		3							3
601-700	2f				1f				3
701-800	2f	1f	1f						4
801-900	2f		1f				1f		4
901-1700	2f	1							3
1701-3400	2f	—	1f			1			4
Totals	14	12	5	4	1	3	1	1	41

The size index for the 1954 progeny at the end of its first growing season ranged from 2 to 190 inches. The distribution of these plants according to size index and chromosome number is given in TABLE IV. The coefficient of correlation between size index and chromosome number was calculated using ungrouped data and it was found that $r = -.3392$. Using the t method r was found to differ significantly from zero with $P = < .05$. The data were further analyzed by testing the linearity of the regression of size index on chromosome number using the analysis of variance method. A variance ratio = 1.107 was obtained which, when compared with $F_{95}(40,10) = 2.08$, is declared not significant indicating the regression does not depart from linearity. The regression was further analyzed by testing the independence of size index on chromosome number and at the 5 per cent level of significance the size index was found to be dependent on chromosome number.

TABLE IV. Distribution of the 1954 *Philadelphus* triploid progeny according to size index and chromosome number.

Size Classes	Chromosome Numbers												Totals
	26	27	28	29	30	31	32	33	34	35	36	37	
1-10 ins.		2					1				1		4
11-20		1	1	2	1	2		1					8
21-30		1	3										4
31-40		1	2	1		1			1		1		7
41-50	2		2		1	1			1	1			8
51-60		2											2
61-70	1					1							2
71-80			2										2
121-170	3	2											5
171-220	1				1								2
Totals	7	9	10	3	3	5	1	1	1	1	2	1	44

The vigor relationships of the two progenies are interpreted in the following manner. Some of the chromosomes of *Philadelphus* when present in an extra dose adversely affect the vigor of the individual. The more extra chromosomes an individual has, the greater is the chance of it having an adverse combination as far as vigor is concerned and thus we find a negative correlation between size index and chromosome number in the seedlings of the 1954 progeny. Presumably the more extreme combinations are eliminated in the gametic and embryonic stages thus explaining the great departure from expected of the distribution of chromosome numbers in both progenies. Nevertheless, a few vigorous aneuploids do occur, indicating some combinations of extra chromosomes do not adversely affect the vigor of the plant. Turning to the 1951 progeny we see that dwarfs and weaklings have less ability to survive than their more vigorous siblings as the three smallest members of the 1951 progeny in 1953 were the only ones which failed to survive the winter of 1953-54. Now the 1951 progeny had suffered over 50 per cent mortality before the chromosome numbers of the survivors were determined in 1953. If it is assumed that most of these deaths were plants lacking in vigor, then it follows that mortality was greater among the higher aneuploids than among the lower. This would cause a shift of the mean chromosome number of the 1951 progeny toward the diploid level, which is exactly what is indicated when the distribution of chromosome numbers found in the survivors of the 1951 progeny in 1953 is compared with that found in the 1954 seedlings. In addition, the removal of the less vigorous higher aneuploids of the 1951 progeny would decrease the correlation between size index and chromosome number thus explaining the lack of such correlation in the survivors of the 1951 progeny as indicated by statistical analysis.

In 1953 eight members of the 1951 progeny flowered, while in 1954 eighteen plants did so. The distribution of flowering plants according to size index and chromosome number is shown in TABLE III. Most of the flowers were quite ordinary, many were small and a few were teratological.

However, two plants had flowers as large as *P.* "Bicolore," one with a flat pure white corolla, and the other with a cup shaped corolla having a pink spot at the base of each petal. This was the only plant to have the pink petal base characteristic of *P.* "Bicolore." Both these plants promise to be more hardy and vigorous than *P.* "Bicolore" in the New England area.

FORSYTHIA

The triploid parent of the *Forsythia* aneuploids is an artificial auto-triploid ($3n = 42$) of *F. intermedia*. The origin of the triploid is described by Hyde (1951). Like *P.* "Bicolore" the triploid *Forsythia* sets very few seed and only small progenies have been obtained, numbering twenty-six plants in all. One of these plants was started in 1950 from seed obtained by open pollination, but since the triploid *Forsythia* is short-styled and self-incompatible the pollen parents of progenies by open pollination could have been only diploid long-styled species. Seven plants were started in 1951 from seed obtained by pollinating the triploid by diploid *F. intermedia*. The remainder are from seed obtained by open pollination; one was started in 1951, three in 1952 and fourteen in 1953. It is not known whether or not the 1950, '51 and '52 progenies were originally larger. Of the 1953 progeny, however, all the plants which were set out in the field in 1953 were still alive at the end of the 1954 season.

The chromosome numbers of the twenty-six plants were determined using iron aceto-carmine leaf squashes. The results are given in TABLE V.

TABLE V. Distribution of the somatic chromosome numbers in progenies from triploid *Forsythia intermedia*.

Chromosome Number	31	36	39	43	46	47	48	49	50	51	52	53	54	55
1950 progeny O.P.									1					
1951 " $3n \times 2n$				1	1			1		1		2	1	
1951 " O.P.														1
1952 " O.P.				1	1					1				
1953 " O.P.	1	1			2	1		2	2	1	2	1	1	1
Total	1	2	1	2	2	1	1	3	3	2	2	3	1	2

In the *Forsythia* progenies the chromosome numbers are scattered between the $2n$ and $4n$ levels with most individuals lying between the $3n$ and $4n$ levels. This distribution is very different from that of the *Philadelphus* triploid progenies where most individuals had diploid or near diploid chromosome numbers.

The *Forsythia* aneuploids are very variable in morphological characters and several striking and bizarre new forms occurred among them. Representative leaf types taken from the middle part of the largest branch of a plant are illustrated in PLATE I, together with the chromosome number of the plant. If their origin were unknown one might hesitate to include some of these aneuploids in the genus *Forsythia*. Unfortunately most of the plants have not yet flowered.

As with the *Philadelphus* progenies, the lengths of all main stems and branches of the *Forsythia* plants were measured after the 1954 growing season. The measurements from each plant were added together to give a size index for that particular plant. When the size index was plotted against chromosome number, for each progeny, there appeared to be no correlation between size and chromosome number, larger and smaller plants being scattered all along the line. However, two outstanding differences, with regard to vigor, were evident between the *Philadelphus* and *Forsythia* triploid progenies. Firstly, there were no extreme dwarfs among the *Forsythia* plants, and secondly, the range in size index was much greater for the *Philadelphus* plants. In the 1953 *Forsythia* progeny the size index of the largest plant was 5.4 times greater than that for the smallest plant, while in the 1951, $3n \times 2n$ *Forsythia* progeny the size index for the largest plant was 5.3 times greater than that for the smallest. In the 1951 *Philadelphus* progeny measured in 1954 the index for the largest plant was 28 times greater than that for the smallest, while in the 1953 progeny the largest was 95 times greater than the smallest. It is possible that the difference in vigor between the triploid progenies of these two genera is due to the same factors responsible for the difference in distribution of chromosome numbers in their triploid progenies.

DISCUSSION

The chromosome numbers observed in the progenies from triploid *Philadelphus* and *Forsythia* fell into two strongly contrasting distributional patterns with most *Philadelphus* plants having the diploid or near diploid chromosome number while most of the *Forsythia* plants had chromosome numbers between the triploid and tetraploid levels. In an attempt to evaluate the factors producing this discrepancy a survey was made of the literature on triploid progenies and factors affecting their chromosome numbers.

Meiosis in Triploids. The distribution of aneuploid chromosome numbers in the progeny of triploids depends, in the first place, on the distribution of the extra chromosomes of the triploid parent during meiosis. In general it has been found that the extra chromosomes are distributed to the poles at random regardless of whether they pair in trivalents or remain as univalents. This statement is supported by the work of Belling (1921) on *Canna*, Belling and Blakeslee (1922) on *Datura*, Kihara (1924) on wheat, Lesley (1926) on tomato, Dermen (1930) on *Petunia*, Skovsted (1933) on cotton, Sax (1937) on *Tradescantia*, Satina and Blakeslee (1937) on *Datura*, Goodspeed and Avery (1939) on *Nicotiana* and Skalinska (1945) on *Aquilegia*. The failure of a few lagging univalents to be included in the telophase nuclei and the subsequent formation of micronuclei has been frequently observed. This leads to a slight departure from random distribution as observed in our *Philadelphus* material.

Chromosome counts on the microspores of triploids have been of value in indicating the percentage of extra chromosomes lost during meiosis.

Upcott and Philp (1939) present a table summarizing new and previously published information on this aspect of the problem. Their work on three tulip species and one *Tradescantia* species indicates practically no loss of extra chromosomes while the findings of Darlington (1929) and King (1933) on two other species of *Tradescantia* are similar. On the other hand, elimination of 19% of the extra chromosomes was found by Upcott and Philp in one tulip species while other workers have observed roughly 11% loss in *Datura* (Satina and Blakeslee, 1937), 10% in hyacinth (Darlington, 1926) and 10 to 12.5% in three species of *Allium* (Levan, 1936). To this enumeration may be added the findings of Punyasingh (1947) on the microspores of triploid maize where only 1.5% loss was observed, while, on the other hand, elimination of 9.5% of the extra chromosomes was found by Belling (1924) in hyacinth, 11.5% in *Narcissus* (Nagao, 1935), 7% in *Tradescantia* (Sax, 1937), 32% in *Coffea* (Krug and Mendes, 1940), 10.3% in hyacinth (Darlington and Mather, 1944) and 29.7% in rye (Lamm, 1944). It must be remembered, however, that the above calculations indicate deviations which could in part or entirely be due to the failure of microspores with certain chromosome combinations to divide, rather than to any loss of chromosomes at meiosis. Thus, when the method for calculating percentage loss (Upcott and Philp, 1939) is applied to the findings of Giles (1941) on *Tradescantia*, an apparent gain of 9.3% is indicated. Giles suggests deficiencies leading to abortive microspores would be more common in cells having fewer extra chromosomes. Similarly Darlington and Mather (1944) found certain chromosome combinations had been selected against in the microspores of triploid hyacinth.

Triploid Progenies. Since 1908, when Gates reported his discovery of triploidy, a considerable body of literature on the chromosome numbers found in the progeny of triploids has been built up. In 1933 East commented, "When the records of the studies of the progenies of triploids are listed, they prove to be a variable lot," and the work of the past twenty years has not decreased the variability. In an attempt to summarize these findings each case has been assigned to one of seven categories depending on the distributional pattern of the chromosome numbers. In most instances it was obvious to which category one particular case belonged but a few decisions have been highly arbitrary.

GROUP I. To this category have been assigned those progenies whose chromosome numbers are as would be expected if the extra chromosomes of the triploid parent were distributed to the gametes at random and if gametes having different numbers functioned and gave viable progeny equally well. Seldom has a perfectly normal distribution been observed, but the findings of van Overeem (1921) on the progeny from $3n \times 4n$ *Oenothera* approach it. Cases were assigned to this category if they had the expected aneuploid numbers well represented and at the same time showed no great overrepresentation of the euploid members. These include the findings of: van Overeem (1921) on $3n \times 2n$ and $3n$ selfed

Oenothera progenies; De Vries and Boedijn (1924) on $3n \times 2n$ *Oenothera* progeny; Dulfer (1926) on $3n \times 2n$ *Oenothera* progeny; Gairdner (1926) on $3n$ selfed *Campanula* progeny; McClintock (1929) on the progeny of $3n \times 2n$ maize; Darlington and Moffett (1930) on the progeny of $3n$ open pollinated apples; Moffett (1931) on the progenies of $3n \times 2n$ and $3n$ selfed apples; Capinpin (1933) on $3n \times 2n$ *Oenothera* progeny; East (1933) on $3n \times 2n$ *Nicotiana* progeny; Nebel (1933) on the progenies from $2n \times 3n$, $3n \times 3n$ and $3n \times 2n$ apple crosses; Longley (1934) on the progeny of *Euchlaena-Zea* ($3n$) \times *Zea* ($2n$); Dermen (1936) on the progeny of open pollinated Baldwin apples; Ramanujam (1939) on open pollinated $3n$ rice progeny; Bergström (1938) on the progeny from $3n$ apples; Wanscher (1939) on the progeny from $3n$ apples; Upcott and Philp (1939) on $3n \times 2n$ tulip progeny; Johnsson (1942) on $3n \times 3n$ *Populus* progeny; Johnsson (1946) on $3n \times 3n$ *Betula* progeny, and Punyasingh (1947) on the progenies from $3n \times 2n$ and $3n \times 3n$ maize crosses.

GROUP II. The progenies assigned to this group show more or less random distribution of aneuploid numbers as in Group I but, in addition, the formation of unreduced gametes in the triploid results in the appearance of tetraploids when a diploid is the other parent, or in pentaploids when a tetraploid is the other parent. To this class belong the findings of: Lammerts (1929) on $3n \times 2n$ and $3n \times 4n$ *Nicotiana* progenies; Goodspeed and Avery (1939) on $3n \times 2n$ *Nicotiana* progeny; Bergström (1940) on progeny from $2n \times 3n$ *Populus* and Johnsson (1942) on progeny from $3n \times 2n$ *Populus*.

GROUP III. This category includes progenies whose chromosome numbers are mostly at or near the diploid level when the female parent is diploid or near the tetraploid level when the female parent is tetraploid. These include the progenies studied by: van Overeem (1921) from *Oenothera biennis* ($2n$) \times *Oe. lamarkiana* ($3n$); Lesley (1928) from $2n \times 3n$ tomato; Dermen (1930) from $2n \times 3n$ *Petunia*; Gairdner and Darlington (1931) from $2n \times 3n$ *Campanula*; Lammerts (1931) from $4n \times 3n$ *Nicotiana*; Yarnell (1931) from $2n \times 3n$ *Fragaria*; Satina et al. (1938) from $2n \times 3n$ *Datura* and Punyasingh (1947) from $2n \times 3n$ maize.

GROUP IV. As in Group III, the progenies included in this category have mostly diploid or near diploid chromosome numbers but with the difference that in these cases the female parent was triploid. These include studies reported by: Belling and Blakeslee (1922) on *Datura*; Boedijn (1925) on *Oenothera*; Karpechenko (1928) on progenies from $3n$ *Raphanobrassica* selfed and \times *Raphanus*; Lesley (1928) on tomato; Yarnell (1931) on *Fragaria*; Satina et al. (1938) on *Datura*; Mangelsdorf and Reeves (1939) on $3n$ *Zea-Tripsacum* \times *Zeae*; Levan (1942) on sugar beets; Lamm (1944) on rye; Myers (1944) on *Lolium*; Skalinska (1945) on *Aquilegia*; Kerber (1954) on barley and the present study on *Philadelphus*.

GROUP V. Progenies included in this group have mostly tetraploid chromosome numbers and are derived from triploid female parents. They include the findings of: Dermen (1930) on selfed $3n$ *Petunia* progeny; Huskins (1934) on progeny of selfed $3n$ tomato; Janaki-Ammal (1934) on selfed $3n$ egg-plant progeny; Matsuda (1935) on progenies from $3n \times 4n$ and $3n \times 3n$ *Petunia*; Krug and Mendes (1940) on progeny from open pollinated $3n$ *Coffea* and Skalinska (1945) on $3n \times 4n$ *Aquilegia* progeny.

GROUP VI. Triploid progenies having two or more euploid levels greatly overrepresented were assigned to this category. Van Overeem (1921) in progeny from $4n \times 3n$ *Oenothera lamarkiana* found mostly near $3n$ and $4n$ individuals while *Oenothera lata* ($2n$) \times *Oe. lamarkiana* ($3n$) gave plants with chromosome numbers clustered about the $2n$, $3n$ and $4n$ levels. McClintock (1929) from $2n \times 3n$ maize obtained mostly $2n$ and near $2n$ plants plus one $3n$. Navashin (1929) obtained mostly $2n$ and $3n$ progeny from triploid *Crepis*. Dermen (1930) from $3n \times 4n$ *Petunia* obtained near $4n$ and $5n$ progenies. Hollingshead (1930) from selfed $3n$ *Crepis* obtained an extensive aneuploid series but the $2n$ and $3n$ levels were overrepresented. Thompson (1931) from selfed $3n$ wheat hybrids obtained mostly $4n$ and near $4n$ plants but the $5n$ and $6n$ levels were also represented. Nishiyama (1934) in the progeny of $3n$ *Avena* hybrids found the near $2n$ and near $4n$ levels greatly overrepresented. Larter (1937) in $3n \times 2n$ banana progeny found the tetraploid and heptaploid levels overrepresented. Upcott and Philp (1939) in $2n \times 3n$ *Tulipa* progeny obtained only $2n$ and near $2n$, near $3n$ and $4n$ plants. Norden-skiöld (1941) in the progeny of $3n \times 6n$ *Phleum* obtained plants at and near the $5n$ and $6n$ levels. Cheesman and Dodds (1942) from many $3n \times 2n$ banana crosses obtained $2n$, $3n$, especially $4n$, a few $5n$, $7n$ and $8n$ plants but aneuploids were rare. Levan (1942) from $2n \times 3n$ sugar beets obtained mostly $2n$ and near $2n$ plants with a few at and near $3n$, while from $3n \times 3n$ sugar beets all the numbers between $2n$ and $4n$ were found but the $2n$ and $3n$ levels were greatly overrepresented. Einset (1945) from $3n$ open pollinated apples obtained mostly aneuploid progeny between $2n$ and $3n$ but the n , $2n$, $3n$ and especially $4n$ levels were overrepresented. Skalinska (1945) from selfed and open pollinated *Aquilegia* obtained only $2n$, near $2n$ and $4n$ individuals.

GROUP VII. Miscellaneous cases which fit none of the above six patterns have been lumped into this unnatural group. Goodspeed et al. (1926) in the progeny from $3n \times 2n$ *Nicotiana* found a good representation of the aneuploid numbers between the $2n$ and $3n$ levels plus a high percentage of triploids. Lammerts (1931) from $3n \times 3n$ *Nicotiana* obtained mostly $6n$ plants. Longley (1934) from a *Zea* ($2n$) \times *Euchlaena-Zea* ($3n$) cross obtained entirely $3n$ or near $3n$ plants while $3n \times 3n$ gave mostly aneuploids between the $3n$ and $4n$ levels. Matsuda (1935) in a $3n \times 2n$ *Petunia* progeny obtained only $3n$ or near $3n$ plants. Levan (1936) from open pollinated $3n$ *Allium* obtained most of the aneuploids between

$2n$ and $4n$ plus a few higher, but most plants were between the $3n$ and $4n$ levels. Satô (1937) from $3n \times 3n$ *Lilium* obtained all the aneuploids from $2n$ to $3n$ plus a few higher but lower aneuploids and triploids were most frequent. The findings of the present study on progeny from $3n$ *Forsythia* are similar to those of Levan (above) in that most individuals were aneuploids between the $3n$ and $4n$ levels.

An examination of the foregoing data indicates that in some genera, notably *Malus* and *Populus* which are secondary polyploids, the chromosome numbers found in triploid progenies approximate a normal distribution, regardless of whether or not the triploid is the female parent. In other genera, as *Oenothera* and *Zea*, random distribution of the extra chromosomes to the progeny results only when the triploid is the female parent indicating aneuploidy is more strongly selected against in the male than in the female gametophyte. In the cases listed in Group IV, however, aneuploidy is selected against even when the female is triploid. It is also evident that, in the majority of triploid progenies, euploidy is highly favored sometimes to the almost complete exclusion of the aneuploids, or, as in *Crepis* and sugar beets, the euploids are accompanied by a high percentage of aneuploids.

Attempted explanations of these phenomena have favored the theory of gene balance elaborated by Bridges (1922). It is assumed that the genetic complement of a normal diploid is such as to permit the individual to develop and function as an integrated organism. Additions of whole genomes to the basic complement affect but little this gene balance, and hence the lower euploid levels in triploid progenies are not markedly selected against. The effect of the addition of extra chromosomes depends upon the genic content of these chromosomes and how the extra genes affect the gene balance of the individual. Thus the long chromosomes of hyacinth, for example, behave as if they each possessed an internal gene balance (Darlington and Mather, 1944) so that presumably any number and combination may be added to a diploid without greatly disturbing the gene balance of the organism. An extensive series of aneuploid hyacinths is known in cultivation. Similarly the recent work of Avers (1954) indicates the chromosomes of *Aster* possess a high degree of internal balance. However, in most cases gene balance is not realized within individual chromosomes so that, as first suggested by Winkler (1916), aneuploids are likely to differ more from diploids than are polyploids.

The triploid progenies which deviate greatly from expected in the distribution of their chromosome numbers probably do so because the extremely unbalanced combinations have been eliminated in the gametic and embryonic stages. The degree of gene unbalance in the remaining viable aneuploids is presumably reflected in the vigor of the plants. Thus the occurrence of a high proportion of vigorous aneuploids in the *Forsythia* progenies suggests many of the chromosomes of this genus possess a high degree of internal gene balance making possible many vigorous high aneuploid combinations. The reverse would be true for *Philadelphus* and other genera where aneuploidy is associated with lack of vigor. Such an

association has been most beautifully demonstrated in sugar beets (Levan, 1942) where curves for the mean weight of tops and roots for each chromosome number reach maxima at the $2n$, $3n$ and $4n$ levels with minima midway between each peak. Similar observations on the vigor of triploid progeny have been made by Levan (1936) on *Allium*, and by Bergström (1940) on *Populus*.

The frequent lack of vigor in aneuploid plants is a drawback to the use of aneuploidy in plant breeding. However, aneuploids are often as variable in vigor as in morphological characters so that Johnsson (1942) found an occasional vigorous aneuploid *Populus* and Nebel (1933) reported a few vigorous aneuploid apples although most such apples are very poor in vigor as emphasized by Crane and Lawrence (1930, 1934) and Einset (1948). Similarly vigorous aneuploids occurred among our *Philadelphus* and *Forsythia* plants giving ample indication of the value of aneuploidy in the production of new and exciting horticultural plants.

SUMMARY

Chromosome numbers were determined for two progenies from a triploid *Philadelphus*. In both progenies the distribution of the numbers was found to be strongly skewed toward the diploid level. Statistical analysis indicated a negative correlation between vigor and chromosome number in the one-year-old progeny, but this correlation had been lost in the four-year-old progeny, presumably due to the death of unbalanced weaklings.

Similarly chromosome numbers were determined for five small progenies from a triploid *Forsythia*. Contrasting to the situation in *Philadelphus* the chromosome numbers in the *Forsythia* progenies were scattered between the diploid and tetraploid levels with most individuals between the triploid and tetraploid levels. No correlation between vigor and chromosome number was evident in the *Forsythia* aneuploids.

The results are interpreted as indicating that the chromosomes of *Philadelphus* possess a low degree of internal gene balance for viability factors, contrasting with the situation in *Forsythia* where a high degree of internal gene balance for viability factors is postulated.

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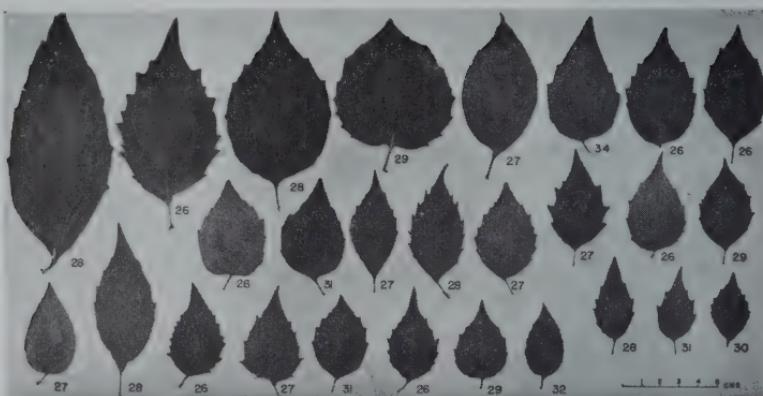
YARNELL, S. H., 1931. A study of certain polyploid and aneuploid forms of *Fragaria*. *Genetics* **16**:455-489.

EXPLANATION OF PLATE I

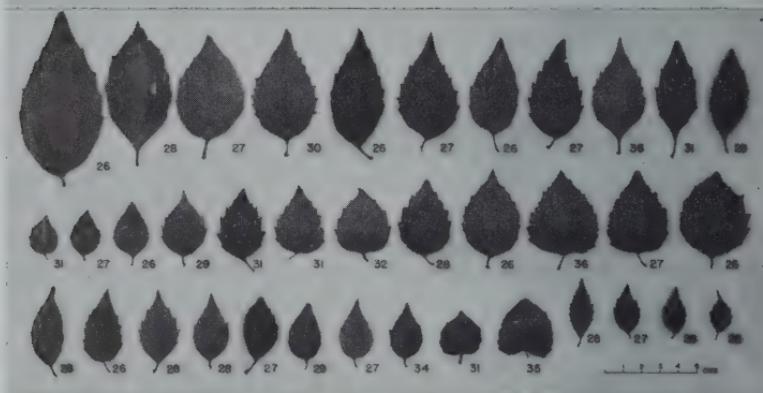
TOP. Representative leaf types of the 1951 *Philadelphus* triploid progeny. The numbers indicate the somatic chromosome number of the plant from which the leaf was taken.

CENTER. Representative leaf types of the 1954 *Philadelphus* triploid progeny. The numbers indicate the somatic chromosome number of the plant from which the leaf was taken.

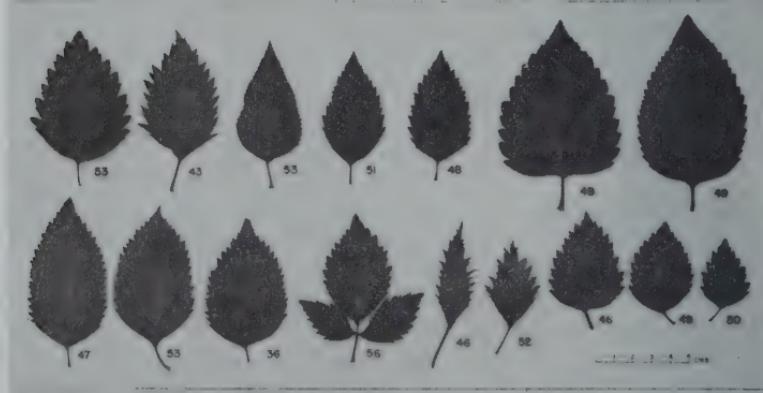
BOTTOM. Representative leaf types of the *Forsythia* triploid progenies. Top row, left to right: 1-5, 1951 $3n \times 2n$; 6, 1952 O.P.; 7 and entire bottom row, 1953 O.P. Numbers indicate somatic chromosome number of plant from which leaf was taken.



PHILADELPHUS 1951 PROGENY



PHILADELPHUS 1954 PROGENY



FORSYTHIA PROGENIES

GEOGRAPHICAL DISTRIBUTION OF THE EUPOMATIACEAE

A. T. HOTCHKISS

WITH THE RENEWED INTEREST, in recent years, in the anatomy, morphology and inter-relationships of members of the ranalian group of angiosperms, the genus *Eupomatia* remains outstanding as one of these plants which has not been intensively reinvestigated in the light of the newer discoveries and interpretations in this field.

In the present paper the history of the classification and the geographical distribution of *Eupomatia* are discussed.

The genus *Eupomatia* R.Br. forms the monogeneric family Eupomatiaceae. *Eupomatia* was discovered by Robert Brown in the colony of Port Jackson (Sydney, N.S.W.), Australia, while he was acting as naturalist on the voyage of M. Flinders to Australia in 1802-03. Brown's description (5, 6) of the genus and species which he named *E. laurina* appear in the Appendix and illustrations by F. Bauer in the Atlas of Flinders' account of his voyage.

In assigning the new genus to a family, Brown observed, "This genus forms a very unexpected addition to Anonaceae, of which it will constitute a distinct section, . . . the affinity . . . is chiefly determined by the structure of the seed." Brown gave as his locality, "woods and thickets in the colony of Port Jackson, especially in the mountainous districts, and on the banks of the principal rivers. . . ."

The second species, *E. bennettii* F.v.Muell., was first described by W. J. Hooker (21) in an illustrated article in Curtis's Botanical Magazine, under the name of *E. laurina* R.Br. His material, blooming plants about a foot high, were supplied by the Messrs. Henderson who had apparently forgotten the precise source of origin of the plants. A handwritten marginal note in this number of Curtis's Botanical Magazine in the library of the National Herbarium at Sydney, N.S.W. is significant —

The plant from which this drawing was made was collected by me at Brisbane in June 1854 and sent same year to Mr. Henderson. The description of the plant is correct but that quoted from Brown refers to another plant altogether.

C. Moore.

— and probably explains their origin. In describing the plant Hooker noted that, "there are some differences between our plant and the figures made by Mr. Bauer and description of Mr. Brown, but not sufficient to justify us in forming of it a distinct species."

In 1858, F. v. Mueller described and named this plant (26) citing Hooker's description and figure and pointed out that Charles Moore first introduced it into England. The type specimen in the National Herbarium

at Melbourne bears the information: *Eupomatisa bennettii* Ferd. Mueller, Moreton Bay, Dr. Mueller.

Another plant first described as a species of *Eupomatisa*, is *Himantandra belgraveana* (F. v. Muell.) F. v. Muell., the nomenclature of which is reviewed by A. C. Smith (28).

The genus *Eupomatisa* was separated from the family Anonaceae and placed in an independent, monogeneric family, the Eupomatiaceae, by L. Diels in 1912 (8). Following Robert Brown's somewhat tentative disposition of the genus in 1814, *Eupomatisa* had been placed in the Anonaceae by Meisner in 1836 (24) who referred to it as a deviationist genus; Endlicher in 1839 (10) under *Anonaceis affines*; Mueller in 1858 (26) under the *Eupomatiaceae*; Bentham and Hooker in 1862 (4) under the tribe *Miliuseae*; Baillon in 1871 (2) who referred to *Eupomatisa* as an aberrant genus; Engler and Prantl in 1891 (14) under the *Eupomatiaceae*, but in 1908 (15) and 1909 (11) under the sub-family *Eupomatioideae*. On the other hand, Bartling in 1830 (3) in emphasizing the affinity of the Anonaceae with the Myristicaceae, assigned *Eupomatisa* to the latter family.

After 1912, botanists generally have followed Diels' lead, and among the supporters of this change are Engler and Gilg (12, 13), Hutchinson (22), Garratt (17), Lemesle (23), Bailey and Nast (1), Ozenda (27), Metcalfe and Chalk (25), and Gundersen (18). Of these authors, the systematists Engler, Hutchinson and Gundersen give the Eupomatiaceae a place close to the Anonaceae, while Garratt, Lemesle and Ozenda emphasize the anatomical differences between the two families and suggest a more distant connection.

SUMMARY OF NOMENCLATURE

EUPOMATIACEAE Diels in Bot. Jahr. 48 (Beibl. 107): 7-13. 1912;
Engler and Gilg in Syl. Pfl. 193. 1912 and 197. 1919; Hutchinson,
Fam: Fl. Pl. Dicot. 88. 1926; Gundersen, Fam. Dicot. 63. 1950.

EUPOMATIA R. Brown in App. Flind. Voy. 2: 597, t. 2. 1814.

Eupomatisa laurina R.Br. in App. Flind. Voy. 2: 597, t. 2. 1814.

Eupomatisa bennettii F. v. Muell. in Muell. Fragm. Phyt. Austr. 1: 45.
1858; Hook. in Bot. Mag. 81: t. 4848. 1855.

GEOGRAPHICAL DISTRIBUTION OF EUPOMATIA

The family Eupomatiaceae occurs from eastern Gippsland, Victoria, to the Cape York peninsula, Queensland, and New Guinea. Along the eastern coast of Australia it is found on the comparatively narrow strip of land lying between the Dividing Range and the coast. In only a few places as at Murrurundi, New South Wales does *Eupomatisa* grow as far inland as a hundred miles from the sea, but in several places as Shoalhaven River, Tenterfield, Tooloom Scrub, New South Wales, and Toowoomba, Queensland, it is found close to the Dividing Range. In New Guinea also, *Eupomatisa* has been found in coastal or near coastal areas.

From the southern limit of its range near the Snowy River in Victoria, *Eupomatia* occurs more or less continuously along the coast of New South Wales in favorable situations which combine shelter, warmth (probably frost-free), moisture and good soil. Areas with these conditions are found usually at low altitudes in coastal gullies, along coastal rivers and on forested escarpments facing the sea. Here *Eupomatia* is found growing as an undershrub or small tree in the shade of a forest which may be called transitional between the sclerophyll forest of the drier slopes and the true rain-forest. The rarity of such favorable situations to the west of the Dividing Range probably accounts for the restriction of *Eupomatia* to the coastal side. In northeastern New South Wales and in Queensland *Eupomatia* may follow the transitional rain-forest up from the gullies on to the flanks and tops of mountains as in the Nightcap Range and Tooloom area of New South Wales, and the Lamington Plateau and other mountains near Brisbane. In the Cairns area, *Eupomatia* is found on the Atherton Tableland and in New Guinea most collections are from mountainous areas.

Of the two species of *Eupomatia*, only *E. laurina* extends to the full limits of this distribution. The range of *E. bennettii* falls within that of *E. laurina*, but it is restricted to northeastern New South Wales and Queensland. Within this section the two species apparently have an identical distribution.

The known localities for *E. bennettii* are indicated on the distribution map, FIG. 1,¹ as solid black triangles.

Between south-eastern Queensland and the Cairns area the known distribution of *Eupomatia* appears to be very intermittent with wide blank spaces. These blank spaces may be due partly to lack of intensive collecting in these areas but are mainly due to the intermittent occurrence of favorable habitat areas. The distribution of Australian rain-forests is discussed in detail by Francis (16) who points out that the moist rain-forest areas are interrupted by drier areas indicated by a predominance of *Eucalyptus* or *Acacia* spp. North of the Cairns area only one specimen was located which would justify including Cape York Peninsula within the range of *Eupomatia*. One would not expect to find *Eupomatia* in the savannah-forests of Cape York and the nearby Fly River valley of Papua but to be

¹ The map, FIG. 1, showing the distribution of *Eupomatia* is based partly on field observations in Australia and partly on specimens and information from the following herbaria:

A	= Arnold Arboretum Herbarium, Harvard University, Cambridge, Mass.
BRI	= Botanical Museum and Herbarium, Brisbane, Queensland.
GH	= Gray Herbarium, Harvard University, Cambridge, Mass.
LAE	= The Papua and New Guinea Herbarium, Lae, New Guinea.
MEL	= Botanic Gardens and National Herbarium, Melbourne, Victoria.
NY	= Herbarium of the New York Botanical Garden, New York, N. Y.
SYD	= National Herbarium, Sydney, New South Wales.
SYD-U	= University of Sydney Herbarium, Sydney, New South Wales.
UC	= University of California Herbarium, Berkeley, California.
US	= United States National Herbarium, Washington, D. C.

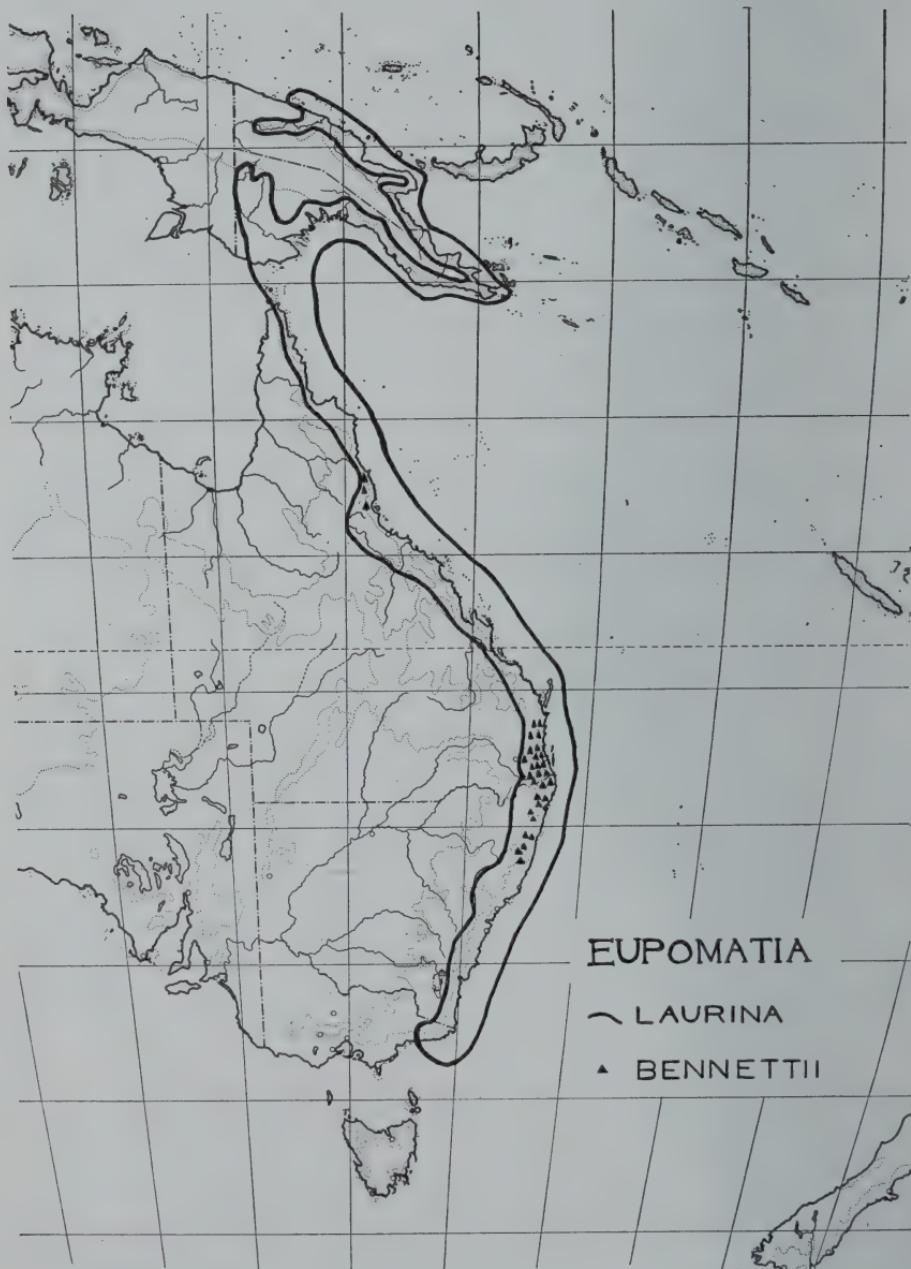


FIG. 1. Approximate known distribution of the genus *Eupomatia*. From Goode's series of base maps, no. 207.

rather widely distributed in the peripheral parts of New Guinea up to an altitude of about 1250 m. In commenting on his collection of *Eupomatia laurina* near Mt. Hagen in the Central Highlands of New Guinea, J. S. Womersley in a recent communication states, "I think it would be perfectly safe to assume that it is throughout the Sepik valley and all tributaries up to 4000 feet." Although there are apparently no records of *E. laurina* from Netherlands New Guinea, it may also be found there when collections from that area are more extensive.

While such a great north-south distribution (about 36°) is shared by a few other genera of Australasian angiosperms, hardly any species extend as far as *E. laurina*. *Hibbertia scandens* (*Hibbertia volubilis*) occurs in New Guinea and down the eastern coast of Australia to southern New South Wales but as this species is at once a member of the strand vegetation and also of the nearby rain-forest margins, its distribution is subject to a different explanation. Although this range for the species *E. laurina* is extensive in latitude, it is a relatively localized one for the genus which is quite restricted in both area and habitat when it is compared with such genera as *Drimys* and *Magnolia*. *Eupomatia* may be found in fairly close association with *Drimys insipida* in coastal gullies and (more rarely for *Eupomatia*) in the Blue Mountains of New South Wales, and again as on Mt. Glorious near Brisbane but not with the sub-alpine species *Drimys lanceolata*, *D. vickeriana*, *D. purpurascens* and *D. stipitata*. The difference in ecological situation can be seen distinctly at Barrington Tops, New South Wales. Here *Eupomatia* is found (with *D. insipida*) associated only with the rain-forest in the gullies at the base of the mountain while at the summit is found *D. purpurascens* associated with such plants as *Nothofagus* and *Gaultheria*. Between these two communities there is a broad zone of sclerophyll forest.

The distribution does indicate that the genus *Eupomatia* has moved across the Torres Strait region between New Guinea and Queensland sometime in the past, and its general ranalian affinities suggest that other more or less related families were doing the same thing at the same time. Under favorable climatic conditions, *Eupomatia* was able to push southward along the eastern coast of Australia until it reached the Southern Ocean. The present discontinuous populations probably represent contractions to smaller areas from a formerly continuous population due to changes in climatic conditions. Crocker and Wood (7), Herbert (19, 20) and others have surveyed the geological history and its consequences on the Australian flora.

In the present case, other evidence such as established close relationships with other families, or evidence from fossils, is vague or lacking. A parallel can be seen in the distribution of the small monogeneric ranalian family *Himantandraceae*, which is found in Queensland and in New Guinea as well as in the Moluccas. Of interest in this connection also are the conclusions and suggestions of A. C. Smith (29) as to the center of origin of the Winteraceae, in pointing to the Queensland-New Guinea area as an ancient home of ranalian plants.



FIG. 2. *Eupomatia bennettii* F. v. Muell. Mature plant showing single, terminal, young fruit and tuberous roots. The dead stubs indicate the position of the fruit in previous years. Near head of small gully, near Bellingen, N.S.W. A. T. Hotchkiss 108, Sept. 3, 1954.



FIG. 3. *Eupomatia laurina* R. Br. Small branch showing flower buds terminal on axillary short shoots about 1 month pre-anthesis. On moist escarpment, Bulli Pass, N.S.W. A. T. Hotchkiss 196, Nov. 27, 1954.

The two species of *Eupomati*, although very distinct, have strong family characters in common. Both have the same number of chromosomes ($N = 10$). Of the two species neither is more primitive in all its features, i.e. some of the morphological details of *E. bennettii* seem to be less specialized than the corresponding form in *E. laurina*. A plant of *E. bennettii* for example usually has but a single flower terminal on the main stem, FIG. 2. *Eupomati laurina*, with smaller flowers, terminal on axillary short shoots, is more specialized in its inflorescences, FIG. 3. On the other hand the tuberous, small (30–60 cm.) shrub *E. bennettii* has the more specialized habit when compared with *E. laurina* which is often a small tree up to 15 m. high. Thus neither should be regarded as being derived directly from the other but rather both species could have been derived from an unspecialized, common ancestor.

Variation within the species is more pronounced in *E. laurina*. A question arises here as to whether *E. laurina* is indeed one and the same species at both north and south extremes of its range. A preliminary comparison of the specimens from the northern Queensland and New Guinea area seems to indicate that they are distinct from the southern population. These differences are found in the leaves, flower buds, flowers and fruits. In the northern population the leaves may be 1.5 to 2 times longer; the flower buds are somewhat larger than the fruits in the southern population, are more nearly spherical, with a slightly elevated calyptra apex (which is conical in southern specimens), and with a more distinctly elongate base below the floral organs; the flowers may have twice as many stamens and staminodes; carpel number has not been determined. Further detailed investigation of the New Guinea material is needed.

In *E. bennettii* variations occur in the size and form of the leaves which range in form from narrow-lanceolate to rhomboidal. But since all these variations have been observed in the offspring of a single plant they are of minor importance.

Both species of *Eupomati* occur in New South Wales and Queensland while *E. laurina* extends southward to Gippsland and northward to New Guinea. The region with the greatest number of species might be considered to be the specific center of origin for the genus. But it should be remembered that both species are in some features relatively specialized and derivative and that both species have the same northern limits in Australia and proximity to New Guinea. It would probably be better to consider *Eupomati* as an element of general Malaysian affinities which has entered Australia and continues to find there suitable ecological niches which give it a somewhat relic distribution along the eastern coastal area.

1. *Eupomati bennettii* F.v. Mueller

DISTRIBUTION: New South Wales; Queensland.

NEW SOUTH WALES: Tirralong, via Bowraville, *G. Garratt* (SYD), 1930.—Bellingen, heads of small ravines, *A. Hotchkiss* (SYD-U), Aug. 15, 1953.—Bellingen-Dorriga road, in timber, *A. Hotchkiss* (SYD-U), Aug. 14, 1953.—Cor-

amba, near Coffs Harbour, *E. Thornton* (MEL), Aug. 8, 1884.—Ulong, half-way from Glenreagh to Dorrigo, *W. Heron* (SYD), 1920.—Clarence River, *E. Betché* (SYD); *H. Beckler* (MEL).—Alstonville, *D. H. Tomlins* (SYD), 1912; (drawing of roots and tubers, SYD).—Richmond River, *F. v. Mueller* (SYD); *Mrs. Hodgkinson* (MEL), 1878.—Tweed River, *W. Guilfoyle* (MEL), 1871; Tweed River, Stokers Siding, *Bray* (SYD), 1937.

QUEENSLAND: Beechmont, *K. Scott* (BRI), 1937.—Springbrook, *A. Salmon* (BRI), 1929.—National Park, MacPherson Range, *A. Hotchkiss* (SYD-U), June 1953.—Tambourine Mountain, *C. T. White* 3569 (A), Aug. 17, 1927; Ibidem, *C. T. White* (BRI), 1916.—Kilcoy, *C. England* (BRI), 1921.—Kelvin Grove, near Brisbane, *J. Shirley* (BRI).—Yandina, *T. P. Keys* (BRI), 1920.—Toowoomba, *C. I. Gwyther* (BRI), 1930.—Moreton Bay, *F. v. Mueller* (TYPE, MEL), July 1855.—Mt. O'Reilly, near Brisbane, *D. A. Goy* (BRI), 1938.—Montville, *J. Shirley* (BRI).—Eumundi, *J. H. Simmonds* (BRI), 1892; *F. M. Bailey* (BRI).—Gold Creek, near Brisbane, *C. T. White* (BRI), 1915.—Nambour, *E. V. McKieg* (BRI), 1930.—Archer's mountain brush, *L. Leichhardt* (SYD), 1843.—Johnstone River, *C. Palmerston* (MEL).—Dalrymple Gap, near Rockingham Bay, *J. Dallachy* (MEL), June 11, 1864.—Danbulla, Atherton Tableland, *L. Smith* (BRI).—Between Cairns and Herberton, *C. J. Wild* (BRI), 1891.

2. *Eupomatia laurina* R. Brown

DISTRIBUTION: Victoria, New South Wales, Queensland, New Guinea.

Victoria: Lower Snowy River, *R. P. Cameron* (MEL), 1895.—Snowy River, *H. B. Williamson* (SYD).—Mt. Buck, near Orbost, *E. E. Pescott* (MEL), Feb. 1901.—Orbost, *J. Rowe* (MEL), 1903.—W. Buck, Gippsland, *C. Walker* (SYD), 1901.—Brodribble River, east Gippsland, *C. Walker*, *E. Pescott* (SYD), 1900.—Wingan and Genoa River (MEL).—Howe Ranges, ca. 2 miles s.e. of Marshmead Homestead on east shore of Mallacoota Inlet, *J. H. Willis* (MEL), Oct. 24, 1948.

New South Wales: Eden, *E. Cheel* (SYD), 1903; *B. Pigott* (SYD), 1931.—Twofold Bay, *F. v. Mueller* (MEL), Sept. 1860; *L. Morton* (MEL).—Tilba Tilba, *E. Reader* (MEL), Jan. 29, 1880.—Mt. Dromedary, *E. Reader* (MEL), Aug. 3, 1880.—Brogers Creek, near Braidwood, *W. Bauerlen* (MEL).—Milton, *R. H. Cambage* 4064 (SYD), 1913.—Shoalhaven River, *F. A. Radaway* (SYD).—Bundanoon, alt. 600 m., *E. F. Constable* 11305 (SYD, US), Jan. 6, 1950.—N. end of Kangaroo Valley, 17 miles from Moss Vale, *R. V. Smith* (MEL), Jan. 28, 1953.—Minnamurra Falls, *L. Johnson*, *H. K. Judd* (SYD), 1953.—Kiama, *W. H. Harvey* (MEL, NY, GH), Jan. 1856.—W. Dapto, *R. H. Cambage* (SYD), 1901.—Mt. Kembla, *A. Hamilton* (SYD).—Bulli, *S. Johnson* (MEL), 1875; *E. Cheel* (SYD), 1900; *A. Hotchkiss* (SYD-U), 1953.—Kissing Point, west of Gladesville, *W. Woolls* (MEL).—North Clifton, *J. J. Fletcher* (SYD), 1893.—Brush Forests, *W. Hudson* (SYD), 1914.—Botany Bay, *G. Caley* (US), Dec. 1804.—New South Wales (no specific locality), *G. Caley* (A), Dec. 29, 1807.—Port Jackson, *R. Brown* 4921 (TYPE, MEL), 1802–1805; no collector (BRI).—North Rocks, Parramatta, *W. Woolls* (MEL).—Blue Mountains, west of Sydney, *L. Atkinson* (MEL), ca. 1860.—Sassafras Gully, Springwood, *A. Hotchkiss* (SYD-U), 1953.—Fox Ground, Kurrajong, (collector not given, MEL).—Barrenjoey Island, Broken Bay, *J. Vickery* (SYD), 1946.

— gully near Gosford, *A. Hotchkiss* (SYD-U), July 1954.—4 miles south of Newcastle (MEL), Dec. 1862.—Crawford River, north of Bulladelah, *E. Cheel* (SYD), 1902.—Tailford to Forster, *J. H. Maiden* (SYD), 1896.—Upper Williams River, near Barrington Tops, *L. Fraser & J. Vickery* (SYD), 1934; *A. Hotchkiss* (SYD-U), Jan. 1954.—Gloucester, *E. Betché* (SYD, MEL), 1882.—Murrurundi, *J. H. Maiden & J. L. Boorman* (SYD), 1902.—Black Creek, near Kendall, *T. Waite* (SYD), 1950.—Kendall, *F. M. Bailey* (SYD), 1929.—Combogne, *E. C. Chisholm* (SYD), 1923.—Port Macquarie, *J. H. Maiden* (SYD), 1897; *H. Beckler* (MEL).—Andersons Sugar Loaf, *J. L. Boorman* (SYD), 1909.—Gleniffer, Bellingen River, *E. Swain & A. Forester* (SYD), 1910.—Bellingen River (MEL); Bellingen River, Bellingen, *A. Hotchkiss* (SYD-U), August 1953.—Coffs Harbour, *J. L. Boorman* (SYD, UC), May 1909.—Bucca Creek, *J. L. Boorman* (SYD), 1912.—Coramba, *J. L. Boorman* (SYD), 1912.—Glenreagh, *A. W. Livingstone* (SYD), 1945.—Clarence River, *J. F. Wilcox* (MEL), Nov. 1875.—Demon Creek, east of Tenterfield, *C. Stuart* (MEL), ca. 1860.—Drake, *J. Richards* (SYD), 1913.—Casino, *D. J. McAuliffe* (SYD), 1913.—Shannon Brook, Casino, *G. Simkins* (SYD), 1914.—Richmond River District, *C. Fawcett* (MEL).—Bangalow, *W. Bauerlen* (SYD), 1896.—Byron Bay, *J. H. Maiden & J. L. Boorman* (SYD), 1903.—Nightcap Range, *A. Hotchkiss* (SYD-U), June 1953.—Beaury State Forest, *C. T. White 12845* (BRI), May 29, 1945; *C. T. White 12843* (A), May 29, 1945.—Tooloom, *A. Hotchkiss* (SYD-U), Dec. 1953.—Between Urbenville and Legume, *A. Hotchkiss* (SYD-U), Dec. 1953.—Tweed Heads, *J. L. Boorman* (SYD, US), Jan. 1914.—Terranara, Tweed Heads, *F. J. Davey* (photo of flowers, SYD), 1906.—Acacia Creek, *W. Donn* (SYD), 1906.—Robbinsville, *R. T. Baker* (US), 1891.

Queensland: National Park, MacPherson Range, *Tryon & White* (A), March 1920; *A. Hotchkiss* (SYD-U), June 1953.—near Emu Vale, MacPherson Range, *W. D. Francis* (BRI), 1920.—Christmas Creek, *D. A. Goy* and *L. Smith 314* (A, BRI), 1938.—Mt. Tamborine, 45 miles s. of Brisbane, alt. 1,800 ft., *C. E. Hubbard 2504* (BRI), May 5, 1930; *J. Shirley* (A); *C. T. White 1772*, (A), Dec. 1921.—Toowoomba, *Hartman* (MEL), 1882.—Laguna Bay, *Eaves* (MEL).—Mt. Glorious, *A. Hotchkiss* (SYD-U), June 1953.—Mistake Mountains, Moreton District, *L. Smith* (BRI), 1948.—Enoggera Creek, *F. v. Mueller* (BRI), 1874; *C. T. White* (BRI), 1914; *F. M. Bailey* (US).—Brisbane River, *F. v. Mueller* (MEL), July 1855.—Brisbane, *Griffith* (MEL).—Pine River, Moreton Bay, *E. Fitzalan* (MEL).—Blackall Range, *C. I. Gwyther* (A), Jan. 1920; *C. T. White* (A), Dec. 1916.—Peeramon, *E. W. Bick* (BRI), 1913.—Palmwoods, *C. T. White* (BRI), 1907.—Gympie, *F. H. Kenny* (BRI), 1907.—Kin Kin, *F. White* (BRI), 1916; *W. T. Francis* (UC), Dec. 1919.—Fraser Island, *C. E. Hubbard 4655* (BRI), Oct. 17, 1930.—Eungella Range, *W. D. Francis* (BRI), 1922; *C. T. White* (BRI), 1938.—Rockingham Bay, *J. Dallachy* (MEL), Feb. 17, 1864, April 13, 1864, Oct. 19, 1864, Sept. 1867, Oct. 28, 1870.—Herbert River, *Eaton* (BRI).—Herberton Range, Scrubby Creek, alt. 600 m. *S. F. Kajewski 1360* (A, NY, BRI), Nov. 14, 1929.—Innisfail, *N. Michael 411* (BRI).—Johnstone River, *H. G. Ladbroke* (BRI), 1917.—Russell River, *W. Sayer* (MEL), 1886, 1887.—Atherton Tableland, *C. T. White* (A, BRI), Jan. 1918.—Kamerunga, *E. Cowley* (BRI), 1892.—Jarra Creek, N. E. Queensland, *A. G. Hanson* (BRI), 1948.—Daintree River, *E. Fitzalan* (MEL), 1876.—Bloomfield River, *W. Bann* (or *Hann?*) (MEL), 1884.

New Guinea: Western Division: Tarara, Wassi Kussa River, common in light rainforest, *L. J. Brass* 8658 (A, LAE), Jan. 1937. Gulf Division: The Cupola, alt. 800 ft., *L. J. Brass* 1362 (A), Jan. 4, 1926. Central Division: Mafulu, forest regrowths, alt. 1250 m., *L. J. Brass* 5218 (A, NY, BRI), Sept.-Nov. 1933. — Sogere, near Port Moresby, *H. O. Forbes* 551 and 547 (MEL), 1885-1886. — Astrolabe Range, *C. T. White* (BRI), 1918. — South East New Guinea (Division?): *J. Chalmers* (MEL), 1885. Morobe Division: Morobe, alt. 3300 ft, *M. S. Clemens* 1975A (A), March 11, 1936. — Kaile, Ogeramnang, alt. 5000 ft., *M. S. Clemens* 5793 (A), April 17, 1937. — Kulungfufu, alt. 5300 ft., *M. S. Clemens* 6527 (A), June 7, 1937. — Busu River, near Lae, *N. G. F.* 5503 (LAE), Feb. 14, 1954. Northeast New Guinea: Baum in den Wäldern am Kaulo, etwa 300 m. ü., blühend, *R. Schlechter* 16870 (UC, also cited by Diels, Bot. Jahr. 49:165, 1913), Nov. 22, 1907. Central Highlands Division, T.N.G.: Baiyer River, near Mt. Hagen, alt. 4000 ft., *N. G. F.* 6799 (LAE), Nov. 25, 1954.

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FURTHER NOTES ON THE WEEDS AND INTRODUCED PLANTS OF FIJI

WILLIAM GREENWOOD

THE NOTES HERE PRESENTED terminate those I have accumulated during 35 years of residence in Fiji, during which much of my spare time was devoted to collecting and studying plants. Other papers in this series have appeared in Proc. Linn. Soc. 154: 92-106. 1943, and in Jour. Arnold Arb. 25: 397-405. 1944, and 30: 75-84. 1949.

In his paper on "The Vegetation and Flora of Fiji" (in Sci. Monthly 73(1): 3-15. 1951), A. C. Smith gives the number of adventive species (weeds, escapes, etc.) in Fiji as 529, and of indigenous species as 1266. This number of adventive species, however, is drawn from all the published records. I feel sure that when the synonymy has been completely checked, and when the species that did not persist have been excluded, this number will be greatly reduced. From my own records I should put the number of adventive species at about 380, or approximately 18 per cent of the total phanerogam flora.

As in my previous papers, families are discussed in the order of Bentham & Hooker's Genera Plantarum. Collection numbers found in the text italicized in parentheses refer to the writer's specimens; these are inserted only when the species has not previously been reported from Fiji.

I was impressed in Fiji by the manner in which a new introduction will increase rapidly for a few years until it covers acres of waste land, to the exclusion of most other plants, subsequent to which it will gradually die down and become no more abundant than dozens of other introductions. This was particularly noticeable among the grasses, which came in, increased rapidly, and then decreased in significance, to be replaced by another grass. Many of the weeds recorded from Fiji on the basis of one or two collections are probably no longer to be found there, and the place of these in lists of the flora is questionable.

NYMPHAEACEAE

Nymphaea capensis Thunb. (probably)

Waimaleka Creek, near Sambeto, Lautoka District, Mba, Viti Levu (1306). This blue-flowered water-lily has been growing in parts of the Lautoka and Nandi Districts for the past 20 years and is quite naturalized. It was probably introduced years ago, since which it has escaped and spread. It is periodically removed from Waimaleka Creek, as its growth hinders the flow of water and tends to cause flooding in nearby sugar-cane lands.

***Nymphaea capensis* Thunb. var. *rosea* Hort. (probably)**

Swamps near Nandi, Nandi District, MBA, Viti Levu (1307). This pink-flowered variety is not as common as the preceding, but it has been quite naturalized in the cited locality for at least ten years.

MALVACEAE***Gossypium* spp.**

In Flora Vitiensis (pp. 21, 22, 1865), Seemann discussed *G. peruvianum* Cav., *G. barbadense* L., and *G. arboreum* L. (with *G. herbaceum* L. as a synonym) as being naturalized in Fiji. They do not appear to have survived, as I have never seen them or heard reports of them in recent years. I believe they should be removed from modern lists of the flora of Fiji.

***Sida acuta* Burm. f.**

In attempting to establish the date of this introduction (in Jour. Arnold Arb. 30: 76, 1949), I remarked that *Greenwood* 99 appeared to be the earliest collection, but I neglected to mention the date of this as 1919.

ZYGOPHYLLACEAE***Tribulus terrestris* L.**

This species is mentioned as occurring in Fiji in Agr. Jour. Dept. Agr. Fiji 11(2): 51, 1940. However, I have never found it nor heard of its collection by recent field workers. The occurrence of *T. cistoides* L. is more to be anticipated in Fiji.

LEGUMINOSAE***Cassia leschenaultiana* DC.**

This plant is becoming common in the MBA and Tavua Districts of Viti Levu, and it has also recently been noted in the Nandi and Singatoka Districts.

MELASTOMATAEAE***Clidemia hirta* (L.) D. Don**

This weed has become fairly common around the edges of clearings in parts of the Mt. Evans Range region, MBA, Viti Levu, at elevations between 2000 and 2500 feet.

CUCURBITACEAE***Coccinea cordifolia* (L.) Cogn.**

The bright red fruits of this creeper are used by the Indians in Fiji in making curries.

COMPOSITAE***Eleutheranthera ruderalis* (Sw.) Sch.-Bip.**

Noticed in waste places around Suva, Viti Levu, in March, 1951.

Erigeron sumatrensis Retz.

This is the species which in earlier papers I discussed as *E. floribundus* (H. B. K.) Sch.-Bip. Some of the specimens referred to *E. albidus* A. Gray may prove to represent *E. sumatrensis*.

BORAGINACEAE

Cynoglossum amabile Stapf & Drummond

Commonly grown in European gardens in Fiji and evidently recently escaped in the vicinity of Nandarivatu, where Smith collected it in 1947 (cf. Jour. Arnold Arb. 33: 116. 1952).

ACANTHACEAE

Thunbergia grandiflora Roxb.

The inclusion of this species in the Fijian flora is questionable, as I feel fairly certain that the locality of Degener's collection in Ra (cf. Sargentia 1: 117. 1942) used to be a garden attached to the District Commissioner's house. Because of its attractive flowers this creeper is commonly grown in European gardens throughout Fiji, but I have never seen or heard of it setting fruit.

Asystasia gangetica (L.) T. Anders.

The seeds of this plant are sought after and eaten by domestic fowls in Fiji.

EUPHORBIACEAE

Euphorbia cf. australis Boiss.

This species, of which the precise identity still remains uncertain (cf. Jour. Arnold Arb. 25: 402. 1944), has now spread from Singatoka to the Lautoka District.

Euphorbia drummondii Boiss.

This species became established on the Colonial Sugar Refining Company's tennis courts at Lautoka, Viti Levu, in 1942. These courts are kept under couch grass (*Cynodon dactylon* Pers.) and are rested each year during the wet season, from about the end of the year until the end of April. By March, 1943, the *Euphorbia* had covered about one quarter of the courts, and in some places it had completely killed the couch grass in patches up to two feet in diameter. As it spreads close to the ground, the regular mowing had no effect on it, and it was necessary to dig up the plants by hand.

HYDROCHARITACEAE

Hydrilla verticillata (L. f.) Royle

During the dry season, when the Nandi River is low, horses wade out into the river and feed on this species, which was first reported from this locality by me in Jour. Arnold Arb. 25: 403. 1944.

GRAMINEAE¹**Andropogon nodosus** (Willem.) Nash

At sea-level, Lautoka, Mba Province, Viti Levu (1223). This species was first noticed about 1950, often at the sides of drains and in other wet places.

Chloris inflata Link

At sea-level, Lautoka, Mba Province, Viti Levu (1213). The species also occurs in the vicinity of the Nandi airport, in the present Mba Province.

Eriochloa procera (Retz.) C. E. Hubbard

Noticed at sides of roads and in waste places around Suva in March, 1951.

Dactylis glomerata L.

This species was originally recorded, as to its Fijian occurrence, from Nandarivatu, Mba Province, Viti Levu, but during various visits there I have never seen it. If its persistence is not indicated by recent collections, it should perhaps be omitted from the lists of the Fijian flora.

Bambusa sp.

The common bamboo in Fiji grows beside creeks and rivers at elevations up to 2000 feet. It is used by the Fijians for rafts, house-building, and numerous other purposes. It is included here because it can be a nuisance. In the wet season, when the Rewa and Singatoka Rivers are liable to flood, clumps of this bamboo growing on the river-banks are undermined and fall into the rivers. They are carried down and, because of the length of the culms (often 60 feet), lodge across the piers of bridges downstream. This causes debris to pile up against the bridges and holds the water back, threatening damage to the piers and superstructures. In such cases it has been necessary for workmen to cut the lodged bamboo culms. To avoid this situation, each year about September workmen are employed to work up the rivers and cut down any large bamboos growing on the banks.

During thirty years of residence on the northern coasts of Viti Levu I have never seen this bamboo in flower and so have never been able to collect material adequate for specific identification. I am told that it flowers frequently on the wet side of Viti Levu.

This species is planted beside tracks by the Fijians for shade, and often on the tops of hills as well. I believe that when so planted it is intended to show the route of a track, as I know of a number of cases where, on coming to the top of a ridge with its clump of bamboos, one can look out and see another clump on a ridge three or four miles away, which one will find to be also beside the track.

¹ Two of the grasses listed here are first reported from Fiji, as indicated by my collection numbers. I am indebted to Dr. Jason R. Swallen for identifications of my recent grass collections.

The species has been in Fiji at least fifty years, and probably longer. I regard it as introduced, possibly from India, by Indians when they first came to Fiji.

I am indebted to Mr. Walter Freeman, of the Colonial Sugar Refining Company, who lived for many years along the Rewa River, for much of the above information.

WAITARA, SYDNEY,
AUSTRALIA.

THE DIRECTOR'S REPORT

THE ARNOLD ARBORETUM DURING THE FISCAL YEAR ENDED
JUNE 30, 1955

On July 1, 1954, the start of the fiscal year, the staff of the Arnold Arboretum was actively engaged in the process of moving the non-horticultural specimens and books from its herbarium and library and its non-horticultural activities to the Harvard University Herbarium in Cambridge. The background for this move was reviewed in the Annual Report for the year 1953-54 (Jour. Arnold Arb. 35: 367-381. 1954). Before the move was attempted, the facilities and activities in horticulture which continue to be centered in the Administration Building in Jamaica Plain were reorganized. The books to remain in Jamaica Plain, forming the horticultural library, were segregated. Herbarium specimens needed for the study of plants under cultivation in the living collections of the Arboretum and elsewhere were organized into a unit located on the main floor of the Administration Building.

The actual moving of specimens and books to Cambridge was completed on July 9th. Plans were then completed for the proper utilization of the Administration Building in Jamaica Plain and a contract was signed for alterations in that building. The improvements were finished in late October. The changes are many and represent a new unit of greater usefulness and efficiency both for the staff of the Arboretum and the general public who wish to consult the horticultural herbarium or library or to take part in the activities of the Arboretum. The horticultural library has been established on the first floor in the front part of the building. A spacious reading room, attractively decorated, is lined with steel shelves for volumes and folios. New fluorescent lighting makes this a pleasant room for library purposes. Additional steel stacks were erected on the second floor for the periodicals applicable to horticulture. Three new offices for the director, the horticulturist and the horticultural secretary open off the library reading room. These rooms supply private offices for these staff members for the first time. The convenience of this business office on the first floor and adjacent to the front door has received the compliments of the many visitors who apply for driving permits and who formerly had to climb a flight of stairs. The front hall has been completely redecorated with new display cases for Arboretum publications and flowering displays. New kodachrome prints of flowering shrubs and trees of the Arboretum have been arranged on the walls.

The other large room in the front part of the building on the first floor has been redecorated and functions both as a lecture hall and a demonstration room. For lectures it is used for some of the education classes conducted by the staff and for meetings of garden clubs and similar groups in connection with Arboretum activities. Such a room has been sorely needed

by the Arboretum for the proper demonstration and conduction of its activities in the field of horticulture. A generous gift from Mr. Godfrey Cabot helped finance the alterations in this room, which is attractively decorated in a light gray-green color with deep crimson draw curtains. It has been approved by officials of the City of Boston as a meeting place for audiences of 100 to 150 persons. It is our desire to maintain this room as a flexible space; hence folding chairs, movable tables and partitions enable the room to be used for lectures, classes and exhibitions. The continuous use of this room by individuals and groups interested in the horticultural work of the Arboretum has proved its value.



FIG. 1. The Harvard University Herbarium in Cambridge, Massachusetts, which houses a portion of the collections of the Arnold Arboretum, the Gray Herbarium, the Orchid Herbarium and Library of Oakes Ames, the University Paleobotanical Collections and is adjacent to the Farlow Herbarium and library. The non-horticultural activities of the Arnold Arboretum were transferred to this building during the summer of 1954.

By the removal of the non-horticultural activities to Cambridge, the Administration Building has gained space for current and future activities. Space in the basement formerly used for the storage of herbarium specimens has been turned over to the grounds crews and redecorated for locker rooms and lunch space. The upper floors of the herbarium wing are used in part

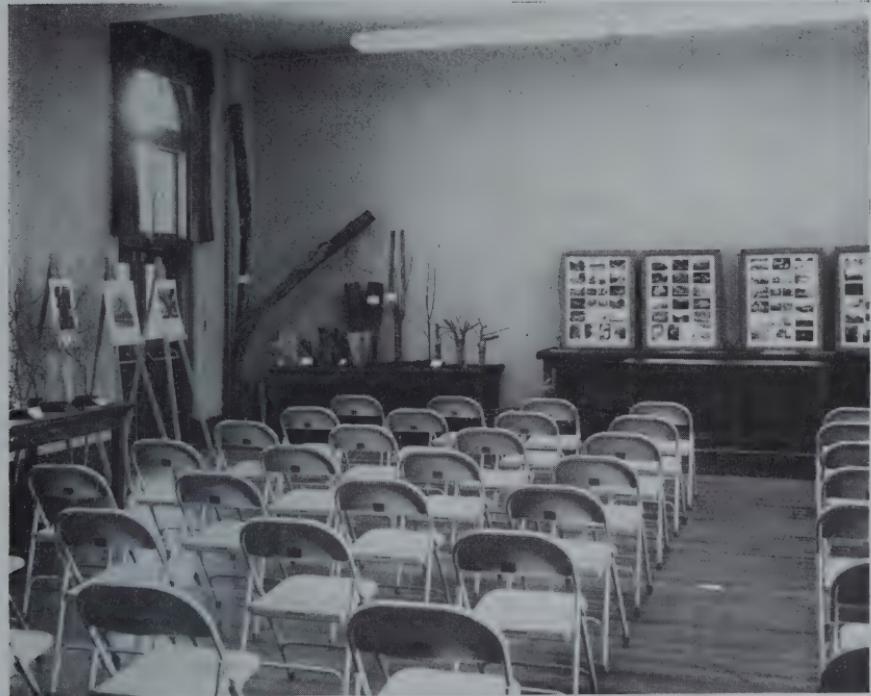


FIG. 2. Top. The new library reading room for horticulture in the Administration Building of the Arnold Arboretum in Jamaica Plain. Three offices open off the left of the reading room. Additional library stacks are located in the rear of the Administration Building.

FIG. 2. Bottom. A portion of the lecture and demonstration room recently created at the Administration Building in Jamaica Plain. Ektachrome display panels are visible on the lecture platform. A portion of the pruning exhibit held in the spring of 1955 is seen at the left. Comfortable folding chairs are available for seating 150 persons.

for active library stack area, particularly periodicals, in part for library storage and in part for storage of unworked herbarium specimens accumulated over the past twenty years. These specimens represent horticultural as well as non-horticultural species and the collections are from China, India, Indo-China, Burma and countries of South America. As staff time permits, these collections will be identified, specimens added to the horticultural or the non-horticultural herbarium and duplicates distributed to other organizations. This accumulation of unworked material represents a sizable investment of Arboretum funds and will involve several thousand hours of professional staff time before the study of them is completed.

Three staff members retain offices on the upper floors of the building. The rooms formerly occupied by the library are empty at the present time and available for increases either in the staff or the horticultural activities of the Arboretum.

Concomitant with the establishment of distinct and organized resources for the field of horticulture, the Arboretum has been able to establish a firmer foundation for the work of its staff in the study of plants not under cultivation and in the native floras of the world. The non-horticultural specimens and books moved to Cambridge, now properly housed in Cambridge in steel cases in a dust-free building under controlled environmental conditions of humidity and temperature, are available for more efficient use by the staff of the Arboretum and by professional colleagues at Harvard and elsewhere. The relatively short distance between the Arboretum's horticultural collections at Jamaica Plain and its non-horticultural collections in Cambridge allows easy interchange of materials and ideas. In Cambridge the Arnold Arboretum's collections are housed for the first time in the same building with the Arboretum's wood and pollen slide collections, the Gray Herbarium, and the paleobotanical collections; and these are adjacent to the excellent facilities of the Museum of Comparative Zool-
ogy, the Botanical Museum and the Biological Laboratories. Already these combined and adjacent collections have proved mutually advantageous and useful to Arboretum staff members, as well as to those of the other institutions and to visiting botanists. The Arboretum's books and specimens are being used more than ever before, to the benefit of all.

With the completion of the physical rearrangements in Jamaica Plain, the majority of the herbarium staff turned its attention to the collections of specimens and books which had been moved to Cambridge. The Gray Herbarium had completed its move before any materials were removed from Jamaica Plain. The books of the Gray Herbarium had all been placed on steel shelving occupying one side of the library stack area. Before the books of the Arboretum were transferred to Cambridge they were all carefully catalogued and each book, pamphlet, folio volume or reprint was properly identified with an embossed seal of the Arnold Arboretum on the fly leaf and on several selected pages in the volume. The inner cover face bore a bookplate of the Arnold Arboretum and labeled on the back of many of the books was the inscription, "Library of the Arnold Arboretum." All books as they are bound or rebound are to be so inscribed. Pamphlets and

similar items bear or will bear an adhesive sticker with the same inscription. The books were arranged on the steel shelves of the other half of the library stack area in the same arrangement which they previously had. Folio volumes are located on special steel folio shelves at one end of the library stack area and are retained in a horizontal position. During the months which have elapsed since the completion of the move of those books to Cambridge, primary attention has been given to correct cataloguing and to the condition of the books. Already we can notice improvement in the condition of the books under the controlled humidity and temperature. Bindings treated in the usual library fashion are holding up better than before.

In planning the moving of the herbaria of the Gray Herbarium and the Arnold Arboretum, it was decided to incorporate the two collections in one phylogenetic sequence based on a modified Engler-Prantl system of classification. This was the system previously used by both herbaria. The adoption of a single sequence instead of maintaining two independent herbaria in the one building was based on our future plans for integration of the two collections. As the Gray Herbarium moved first, the cases holding herbarium specimens from that institution were spaced on the floors to house the total herbarium. The 440 new herbarium cases purchased for the building were also spaced in a general floor plan. The herbarium specimens of the Arnold Arboretum previously stamped on each sheet with the seal of the Arnold Arboretum were moved in their cases or in the cardboard boxes which housed these specimens in Jamaica Plain. The specimens in steel cases were interpolated in available space in the new building near the same families of the Gray Herbarium sequence. The specimens in the smaller cardboard boxes were placed on top of the new and empty cases in the approximate proper location in the sequence. The planning was almost one hundred per cent perfect. With the cases in place, each case was carefully aligned and wedged for proper fit with adjacent cases and for proper function and seal. Felts were replaced on nearly all the cases. These felts had been treated with insecticide and each case was reexamined and determined to be insect-free or was fumigated immediately.

During the remainder of the fall and winter months, some of the herbarium staff worked continuously to incorporate those herbarium specimens housed in cardboard boxes into the sequence of classification housed in steel cases. It required 166 of the new steel cases to house properly the Arboretum specimens formerly kept in cardboard boxes. During the spring months the Arboretum staff undertook another long-neglected task, that of inserting the specimens which had been mounted in recent years. At the end of this fiscal year these housekeeping tasks are nearing completion. For the first time in over twenty years all of the Arboretum's organized collections are housed in steel herbarium cases. For the first time in nearly twenty years, all of the Arboretum's organized collections are in one systematic sequence.

There remains ahead for the staff of the Arnold Arboretum and that of the Gray Herbarium the task of placing in association the specimens of

each family, genus and species. While all specimens of a given family are now on the same floor and generally within a few cases or rows of cases from each other, it is hoped to organize these specimens gradually in proper proximity. This is a long task and it is planned to spend several years in completing the process. The major move of two large herbaria and libraries has been completed with only brief interruptions in the availability of the materials. During the move all the normal service and professional activities of the Arnold Arboretum continued without interruption. New programs were started, old programs were maintained. The majority of the staff worked devotedly at the task of maintaining and furthering the preeminent position of the Arnold Arboretum among the institutions of its kind in this country and in the world.

The Staff:

It is with regret that the staff loses through retirement during the past fiscal year two of its members, Professor Irving Widmer Bailey as Professor of Plant Anatomy and Miss Ethel Upham as Herbarium Assistant. Professor Bailey joined the staff of the Arnold Arboretum in 1933 and has been primarily responsible for the development of the wood, slide and pollen collections of this institution. He served as a member of the editorial board of the *Journal of the Arnold Arboretum* from 1941 to the present and was a frequent contributor to the pages of the *Journal* during that period.

Miss Ethel Upham joined the Arboretum staff as secretary in 1945 but her abilities as an editorial assistant and herbarium assistant enabled her to play a contributory role to the many facets of this institution.

In September, 1954, Dr. Carroll E. Wood, Jr., joined the staff of the Arboretum as Associate Curator. Dr. Wood received his Ph.D. from Harvard University and was Associate Professor of Botany at the University of North Carolina immediately before his appointment. With an interest in horticulture and in the flora of the southeastern United States and as a capable teacher and field botanist, Dr. Wood is a valuable addition to the staff. Among his many duties, he is in charge of the adult education program at the Arboretum.

Mr. Roger Coggeshall was appointed head propagator on July 1, 1954, following the resignation of Mr. Lipp.

Honors came to several of the staff members during the past year. Professor Bailey was awarded the Mary Soper Pope award by the Cranbrook Institute of Science at the meeting of the American Academy of Arts and Sciences at Berkeley, California. At the Commencement of Harvard University on June 16th, Professor Bailey was awarded an honorary Doctor of Science degree with the citation, "Today your university salutes you for your direction of botanical study and for your accomplishment in searching, in the anatomy of plants, for clues to the miracle of growth."

Dr. Donald Wyman was reelected a trustee of the Massachusetts Horticultural Society at its annual meeting and Dr. Richard Howard was elected chairman of the nomenclature section of the Ninth International Botanical Congress. Dr. Kobuski was elected to the council of the New England

Botanical Club and also serves as assistant curator of the herbarium of the club.

Members of the staff officially represented the Arnold Arboretum at various scientific and horticultural meetings throughout the country during the year. Dr. Carroll Wood, Dr. Richard Howard and Dr. Hu attended the annual meeting of the American Institute of Biological Sciences at Gainesville, Florida, in September. Dr. Wood served as chairman at one of the meetings and Dr. Howard took part in symposia sponsored by the American Society of Plant Taxonomists on the "Origin of the Coastal Plain Flora" and by the Society for the Study of Evolution on "The Origin and Evolution of the Biota of Florida." Dr. Howard served as president *pro tem* at the annual banquet of the American Society of Plant Taxonomists. Dr. Hu spoke on her work on *Paulownia*.

Professor Bailey represented the Arnold Arboretum at the meetings of the Botanical Society of America and the American Association of Arts and Sciences.

Mr. Roger Coggeshall served as moderator of two symposia at the annual meeting of the Plant Propagators Society in Cleveland. Both Dr. Sax and Mr. Coggeshall presented papers at the New England Regional Meeting of the American Society of Horticultural Sciences held in Cambridge.

Dr. Sax was chairman of a section of the conference on mutations held at the Brookhaven Laboratory in New York and was a consultant at the radiation biology conference held by the Biology Department of the Oak Ridge National Laboratory.

The demand for members of the Arboretum staff as speakers to various meetings was high and it is impossible to list all the groups concerned. Dr. Howard was the principal speaker at the Wellesley College Garden Day program and spoke on "Hurricanes and Horticulture." Dr. Howard also presented one of the downtown lectures for the New York Botanical Garden, where he talked on "Horticultural Highlights of the Caribbean Islands." He talked about the work of the Arnold Arboretum to the Chestnut Hill Garden Club, the Kiwanis Clubs of Jamaica Plain and West Roxbury, the American Begonia Society and to the Tree Wardens of Middlesex County and on other topics to the Garden Clubs of Lowell and West Roxbury, Massachusetts, and the Garden Club of Short Hills, New Jersey, as well as the Womens Club of Worcester, Massachusetts, and of Western Massachusetts. Dr. Wood talked on "Pollination of Plants" at a meeting of the Boston Horticultural Club and of the Gardeners and Florists Club of Boston. Dr. Wyman was one of the principal speakers at the Michigan Landscape Conference of Michigan State College, where he spoke on "New Plants for Contemporary Homes"; at the New York Botanical Garden's Rose Day, where his subject was, "The Wild Roses of the World" and the Rhode Island Shade Tree Conference when he talked on the subject, "Using Trees Wisely." Dr. Wyman spoke to garden clubs in areas ranging from Charlotte, North Carolina, to Durham, New Hampshire.

Mr. Williams spoke to the Milton Garden Club on pruning and Mr. Coggeshall was speaker at meetings of the Garden Clubs of West Roxbury.

New Bedford, Wareham, Marblehead and Cohasset on the subject of plant propagation. Mr. Coggeshall also spoke on the subject of "How an Arboretum Can Aid the Nurseryman" during the short course for nurserymen at the New York Agriculture School at Farmingdale, New York.

Horticulture:

Two devastating hurricanes ripped through the Arboretum in late August and September with Hurricane "Carol" on August 31st doing the more damage. Four hundred trees were either blown down or severely damaged. The ground force was able to pull back to an upright position and thus save approximately 25% of these within ten days of the storm. A brush chipper and two chain saws were bought with funds restricted to hurricane repair to aid in the process of cleaning up the debris. Small consolation for the loss could be found in the fact that the brush chipper supplied mulch for the remaining trees. By early spring most of the downed trees had been removed but the damage to branches will require many additional months of careful pruning and tree repair. Of all the trees blown down in these storms, only seven were not duplicated elsewhere in the collections. Attempts were made immediately to propagate these seven clones. All of the clean-up work was accomplished by the regular ground force, but the emergency made impossible the annual fall planting schedule.

The hurricanes were followed by a severe open winter. Nevertheless, the flowering display on the grounds during the spring months was one of the best in recent years. The dove tree bloomed profusely and with special publicity was sought out by many visitors. Equally outstanding in the quantity of bloom were the lilacs and the rhododendrons. The Dexter Rhododendrons fortunei hybrids on Hemlock Hill have never bloomed as well as they did this year.

Although lilac blight was fairly prevalent in surrounding areas this year, there was practically none in the Arboretum due to timely spraying with Puratized Apple Spray. The same can be said of fire blight on the crab apples which have received experimental treatments with "Agri-mycin" one of the newer antibiotics.

Lawn areas in the Arboretum received special applications of fertilizer this spring and the other collections were continued on the regular rotation program of application of fertilizer. Spraying for insect and disease control has taken a great deal of time, forty-seven man days in the past year, but the collections reflect the extra attention given them.

Two hundred and fifty species and varieties of plants were added to the major collections in Jamaica Plain during the year. Most of these represented plants new to the living collections of the Arnold Arboretum, although a few were planted to replace some of the older specimens. Plant materials collected by Dr. Wyman in Europe in 1952 and since held in post entry quarantine were released during the year and are now being propagated for the Arboretum collections and for distribution. Thirty new varieties of rhododendron were either purchased or given to the Arboretum

and will eventually be added to our rapidly growing rhododendron collection.

Nine new or very rare plants were propagated and distributed to thirty-two nurserymen and botanic gardens in the United States, Canada, England and Holland as a continuation of our important plant introduction and distribution program. This year the plants distributed included *Cytisus praecox luteus*, a dwarf form of the species not otherwise available in America; *Larix decidua pendula*, a plant which we feel should be grown more than it is; a male form of *Phelodendron amurense* which is unavailable currently from commercial sources and a new dark red-flowered bush honeysuckle which originated in the Arnold Arboretum in 1947. In addition, the Arboretum continued its efforts in cooperating with other arboreta in the United States and the Department of Plant Introduction of the U.S. Department of Agriculture to make it possible to obtain from foreign sources certain woody plants which formerly have been forbidden entry. The Arboretum obtained twenty-three species and varieties under this program this year. None of these is currently under cultivation in the United States.

During the past year one hundred and twenty-seven shipments of plant materials of four hundred and seventy-three species and varieties were sent from the Arnold Arboretum to other institutions in nine countries. In addition to the United States, such materials were sent to Canada, England, Japan, Sweden, Israel, Iceland, Holland and Switzerland. In exchange or by special request, subsidy of foreign collectors or by purchase, the Arnold Arboretum received one hundred and forty-nine shipments comprising five hundred and seventy-five species and varieties. These materials came from ten countries on three continents other than North America. Many of the plant materials received must be regarded as experimental in nature for trial under the local growing conditions. While all plants are regarded as excellent ornamental trees or shrubs in the area in which they were collected, not all will grow at the Arboretum. An excellent example is the outstanding Glen Dale Azaleas which have been tried on several occasions at the Arboretum or at the Case Estates. Several years ago an attempt to grow the Glen Dale Azaleas without winter protection resulted in the loss of the entire planting. Last year a similar experimental plot was established and the plants were given normally adequate winter protection. In spite of this, most of the plants were killed or severely injured in what was a "severe" winter for broad-leaved evergreens.

The physical plant for horticulture, both the Administration Building and the greenhouses received special attention during the past year. In addition to the alterations in the rooms of the Administration Building open to the public, the horticultural herbarium was repainted and its appearance generally improved. The basement was cleaned up and locker and lunch rooms established. New safety doors to the buildings were built. At the greenhouse area the greenhouses themselves received new glazing where necessary and the frame work was painted. The class room for the plant propagation classes was established and a major overhaul was accomplished

on the cold pits. Some of the shade and lath frames were destroyed during the hurricanes and these were rebuilt. An automatic ventilating machine was installed in the east greenhouse during the summer of 1954 and the greenhouse benches were made watertight by lining them with asphalt roofing paper. These benches were then filled with sand and chicken fountains modified for automatic watering were set up at the higher ends of the benches. The chicken fountains allowed the water to seep into the sand and the potted plants on the benches were watered from below by an economical and simple system which is semi-automatic in operation. As the cutting benches holding plants to be rooted are under polyethylene plastic film, the greenhouse can now safely operate without care for periods up to three days.

Dr. Wyman taught three classes in the adult education program during the past year and all were well attended. In addition to editing *Arnoldia* and seeing the Arnold Arboretum Garden Book through the final steps of publication, Dr. Wyman found time to supervise the work of the horticultural department and to lecture to many garden clubs. He was asked by the American Association of Botanic Gardens and Arboretums to revise his "Crab Apples for America" which is now being set in type for fall publication by the Association.

Mr. Coggeshall proved himself an inspiring teacher when enrollment required that he offer three sections of his course in plant propagation in the fall and again in the spring. His routine work as propagator resulted in the production of 21,942 new plants for Arboretum activities. Of these, 19,829 were reproduced by cuttings; 1,801 by grafting; 330 by budding and 279 lots of seeds were germinated and processed. With the cooperation of other members of the horticultural staff, various experiments under Mr. Coggeshall's direction were initiated or maintained in the greenhouses. The effects of different hormone treatment and of rooting media are being studied on *Magnolia*, *Stewartia*, *Syringa*, *Azalea* and *Acer*. Various species of *Vaccinium* are receiving controlled treatments for a study of rooting response to different hormone concentrations. An additional study is being made on these vacciniums to determine the advisability of storing the cuttings before rooting is attempted. *Ilex opaca* is also being studied for the effects of rooting response to different hormone concentrations and both before and after over-wintering the cuttings in refrigerated space. Replicate experiments are being run on *Hamamelis*, *Acer*, *Fagus*, *Tilia*, *Aesculus* and *Betula* species to determine the simplest type of grafting procedure possible with these species and to compare the results of graft unions made with polyethylene or waxed string ties. The effects of concentrated sulfuric acid treatment of seeds of species of *Rosa* and *Ilex* as a means of hastening germination is under study, as is the effect of polyethylene plastic on bud take of *Prunus serrula*.

Mr. Heman Howard continued to take colored as well as black and white pictures of the plants of the Arboretum collections and these were added to the reference files in the horticultural library. Mr. Howard was also in charge of the usual winter activity of preparing the wooden display

labels and the metal record tags which are placed on all plants in or added to the living collections. He assisted in the routine activity of checking a third of the Arboretum each year in relation to our maps, which are then redrawn if necessary to bring them up to date.

The entire Arboretum staff takes part in the activities of the Arboretum relating to groups of visitors and the answering of many questions. Horticultural queries came from 27 states and 14 foreign countries during the year, with telephone calls too numerous to count. Identifications of plants sent in for naming are handled by both the horticultural and herbarium staffs. Many queries are received relating to sources of plants normally difficult to obtain. The library collection of nursery catalogues are used to answer such questions, in addition to other more standard source books. Services such as these are time-consuming, but an integral and valuable part of the many services the Arboretum staff can and does offer to the public, to nurserymen and to other professional colleagues.

The Case Estates:

Considerable damage was done to the trees about the Case Estates by the two hurricanes, but such damage was in no way comparable to that felt in Jamaica Plain. The staff was able to clean up and remove the debris, although a commercial arborist was hired to assist in the repair of the trees by proper pruning of broken branches.

A major reorganization was made in the arrangement of the temporary and permanent nurseries to facilitate a land improvement program and to make new plantings easier. Since Weston's New Country School just opened on the land adjacent to the lower field, it has received special publicity and many visitors. To improve the vistas from this school area, the overgrown shrubs and some of the trees in the lower field were removed. This new open area materially increases the beauty of this important and much-travelled portion of the town of Weston. Permission was given to the town of Weston to relocate a portion of the stone wall around the ground cover plots to remove a traffic hazard and improve an access road from town property.

Experimental work continues at the Case Estates. Rhododendrons were sprayed in the fall with either "Dow-wax" or "Wilt-Pruf" and were in excellent condition the following spring, showing neither bad effects from the treatment nor from winter injury. The application of "Wilt-Pruf" appeared to result in a better appearing plant by spring, although it gave no indication of better protection.

Maleic hydrazide was tried as a control of growth of grass and of a *Prinsepia* hedge but without noticeable results. Careful observation has also been made of our practice of using polyethylene plastic film as a wrapping material in packing plants for shipment. Experiments during the past year showed that dormant, bare-root azalea plants kept tightly wrapped in this material for three weeks grew normally when planted. These experiments showed that plant materials sent from the Arnold Arboretum may be expected to grow if handled properly by the recipient.

Land was made available on the Case Estates for continuation of the work of the Cabot Foundation for the growth of poplar, pine and oak and of the Bussey Institution for growing dwarf apple trees and corn.

Over thirty clones of *Rhododendron fortunei* hybrid selections are growing well in the Ericaceous nursery. These have been picked from some of the best plantings in the area from Long Island to Newburyport.

Winter injury again disfigured most of the Deutzias, Spiraeas and many of the Weigelas in the permanent nursery, proving once again the wisdom of growing less desirable record plants at the Case Estates instead of in the major collections in Jamaica Plain. During the spring the *Weigela*, *Philadelphus* and *Deutzia* collection of certified varieties from de Proeftuin te Boskoop, Holland, obtained in 1951, bloomed well and will shortly be valuable for purposes of identification of these groups.

The "Open House" held at the Case Estates on May 7 and 8 was well attended in spite of inclement weather. The interest in the shrub and perennial garden made clear the desirability of placing display labels on all the plants in this garden. Formerly only location maps were maintained for this planting. Interest in the ground cover plots and the small tree demonstration area remained high following the Open House.

The Adult Education Program:

In the fall of 1954 the staff of the Arboretum introduced on a regular schedule an adult education program. The classes, offered for a nominal fee to cover the expenses of the courses, were designed to present to the public interested in horticulture and scientific botany an opportunity to become familiar with topics of interest, as well as with the staff members themselves and the resources of the Arnold Arboretum. Classes were held in the new lecture room at the Administration Building in Jamaica Plain or at the Greenhouses. All of the classes were informal, with no prerequisites and no academic credit given. Each member who attended regularly, however, received a certificate at the completion of the course or a small plant as a "graduation" gift. Many of the classes featured practical laboratory work with plant materials and nearly all called upon the use of kodachromes from the Arboretum's collections to illustrate the materials and methods of the topic. The four courses offered in the fall were Basic Botany for the Home Gardener by Dr. Wood; Fall Field Class in Ornamental Plants by Dr. Wyman; Plant Propagation by Mr. Coggeshall and Tropical Botany by Dr. Howard. One hundred and thirteen students enrolled for these courses.

During the spring semester additional courses were offered to one hundred and fifty-two students. These were Maintenance of the Home Grounds by Mr. Williams; Spring Field Class in Ornamental Plants and The Best Woody Plants for New England, both by Dr. Wyman and Plant Propagation by Mr. Coggeshall.

The staff plans to continue offering adult education classes on these and other subjects in succeeding years. Interest in this informal instruction in horticulture and more basic aspects of botany is growing.

In addition to these courses, the Arboretum staff offered many shorter sessions and conducted tours of the grounds or the facilities of the Arboretum. During the peak of the spring flowering season the staff explained the work of the Arboretum and offered tours of the grounds to thirty-five groups. Groups varied in size from the minimum of twenty-five persons required for a guided tour to the over four hundred persons who attended the annual Field Day of the Massachusetts Horticultural Society at the Arnold Arboretum. Special demonstrations of pruning, plant propagation or other techniques for maintaining trees and shrubs were conducted for the Field Day of the Massachusetts Horticultural Society and for the meeting of the Horticultural Chairmen of the Federated Garden Clubs of Massachusetts.

Exhibits and Displays:

The newly available demonstration room in the Administration Building of the Arnold Arboretum offered to the staff the opportunity of presenting exhibits and displays of plant materials. The first exhibit held during the past year was a display of original paintings of tropical flowering trees and shrubs. The collection of twenty-nine paintings *in tempera* depicted the most spectacular flowering plants of the Caribbean area. The paintings by Bernard and Harriet Pertchik were all included in the book, "Flowering Trees of the Caribbean," published by Rinehart and Company in 1951. The paintings were sponsored by the Alcoa Steamship Company and their loan to the Arnold Arboretum was appreciated by the staff as well as the many residents of New England who saw this exhibit.

During the Christmas season the featured exhibit at the Arboretum was a collection of evergreens for Christmas. The most common evergreen trees and shrubs and those used as Christmas trees or in Christmas greens were on display with appropriate botanical information supplied on labels. Additional displays at the time centered attention on plant materials for wreaths and on the methods of improving the keeping quality of Christmas greens. A large Douglas fir, a victim of the September hurricanes, served as a Christmas tree for the occasion and was decorated with painted fruits and seeds from native plants. The excellent newspaper coverage given this display drew many visitors to the Arboretum during the Christmas holidays.

A collection of outstanding large-sized photographs by Dr. Wyman and Mr. Heman Howard of the best trees and shrubs, formed a display for the early spring months and was replaced in April by an exhibit of pruning methods and materials prepared by the horticultural staff. Many of the trees damaged or destroyed by the hurricanes which swept through the Arboretum the previous fall showed evidences of both good and bad pruning at an earlier date. These plant materials were used to advantage in the pruning exhibit. The example of a tree destroyed because a forgotten guy wire was left in place made a forceful reminder to those visitors who had supported trees in such a manner following Hurricane Carol. Examples of trees which died because of girdling roots or an earlier potbound condi-

tion, as well as trees which suffered rot for lack of protective paint following pruning were used to illustrate proper and improper tree care.

The exhibit of the Arnold Arboretum at the Spring Flower Show of the Massachusetts Horticultural Society featured ground cover plants in a setting designed to show the type of plant to be used for a variety of exposures. The exhibit had a favorable location in the hall and attracted much attention and comment. Again this year the Arboretum was awarded a gold medal for its exhibit.

Mrs. Schwarten prepared special library exhibits for meetings of the Bio-Historical Club and the Harvard University Library Club. Both organizations met in the Harvard University Herbarium and were particularly interested in the library, its management and its resources.

During the annual meeting of the Federated Garden Clubs of Massachusetts held at the New Ocean House in Swampscott, Massachusetts, the Arboretum exhibited a collection of flowering trees and shrubs as well as ektachrome display panels. As two other conventions were in progress in the hotel during the course of this exhibition, the plants received unexpected attention.

The Arboretum was fortunate during the year in having excellent co-operation from the newspapers, radio and the television stations in publicizing all of its activities, as well as the flowering season at the Arnold Arboretum. Without this cooperation our attendance would not have reached the gratifying stage it did. Over 300 newspaper or magazine clippings (or notices) about the Arnold Arboretum have accumulated during the year. Channel 2, Station WGBH-TV, through its "Images" program, featured the plants of the Arboretum by using kodachrome slides from the Arboretum collection. While we all wished colored projection were possible to bring out the full beauty of both the slides and the plants, the inquiries following these programs indicated a receptive audience.

The Arnold Arboretum staff served as hosts to visitors at two well publicized "Open Houses." On December 17 and 18 an "Open House" was held at the Administration Building in Jamaica Plain and in spite of inclement weather a sizable group attended to inspect the alterations in the building and to see the exhibits. On May 7 and 8 an "Open House" was held at the Case Estates in Weston. Parking became a problem on both of these days on the narrow Weston road, for the location of the Case Estates is away from public transportation. Our best estimates are that 3000 people visited the Case Estates during those two days and were particularly interested in the perennial garden, the woods garden, the ground cover plots and the various nursery collections of new introductions. It is our hope that annual open houses can be conducted at both Jamaica Plain and at the Case Estates in future years.

Library:

The actual move of the larger part of the Arboretum library to the new quarters in the Harvard University Herbarium in Cambridge was completed in the first month of the past fiscal year. During the remain-



FIG. 3. Top. A portion of the reading and reference room in the Harvard University Herbarium.

FIG. 3. Bottom. The center aisle of the library stack area in the Harvard University Herbarium in Cambridge. The Arboretum books are on steel shelving in an air-conditioned building where humidity is controlled and dust is filtered from the air.

ing portion of the past year Mrs. Schwarten, the librarian, capably assisted by other staff members, has devoted her time to rearrangement, labelling, cataloguing and reconditioning the books in both the horticultural library in Jamaica Plain and the non-horticultural library in Cambridge. It is with gratitude that acknowledgment is made of the efficient and devoted care being given the books of the Arnold Arboretum. Throughout the move, routine library activities were unhampered and requests for inter-library loans, assistance to staff members attempting research and consideration of interested visitors were accomplished.

At the completion of the new library quarters in the Administration Building in Jamaica Plain, the books and reference volumes were arranged on steel shelves in the reading room on the first floor. A special table is devoted to the display of current periodicals as they are received and back numbers of current volumes are on special shelves and readily available. On the second floor of the Administration Building, steel shelves were erected to accommodate the bound volumes of periodicals dealing with horticulture and horticultural subjects. A complete card catalogue of all horticultural holdings, including a periodical catalogue, is maintained.

The major task of arranging on steel shelves the books moved to Cambridge was accomplished through efficient and flawless planning. These books are receiving continuing attention for correct placement, cataloguing and labelling. All volumes are being cleaned and bindings are being treated as required. A master card catalogue is maintained to indicate horticultural holdings in Jamaica Plain as well as those volumes in the non-horticultural library. During the past year 536 volumes were added to the libraries either by gift, purchase, exchange or binding, bringing the accessioned total number to 49,209. Pamphlets received and added to the library collections numbered 340, bringing the total to 15,750. One thousand nine hundred and seventy-five catalogue cards were added to the master catalogue and 4066 cards to the Gray Herbarium species card index.

The library of the Arnold Arboretum received many useful gifts of books, pamphlets and photographs during the past year. It is a pleasure to acknowledge the gift mentioned elsewhere from Mr. and Mrs. F. H. Palmer, as well as particularly fine gifts from Mr. Arthur Shurcliff and Mrs. Roy Arthur Hunt. Mr. Shurcliff presented a copy of Miller's Gardener's Dictionary and Mrs. Hunt a gift which included two manuals of Gardening from English manuscripts in her own collection. The library of the Arnold Arboretum also received from the Baker Library of the Graduate School of Business Administration a collection of thirty botanical volumes from the Winthrop collection in particularly fine bindings.

Frans Verdoorn, Research Associate, spent much time, during the past year, on the preparation of a revised edition of his *World List of Plant Science Institutions*. The new, fifth edition will include more than twice as many entries as the fourth edition of 1938.

Work on the biographical card index of plant scientists, being prepared as a basis for the *Index Botanicorum*, continued as in previous years, with

the aid of three assistants. The index consists now of about a million cards.

Work towards an annotated bibliography on *Linnaeus and his Time* was continued in an effort to display Linnaeus' life and manifold activities in their full historical context.

Herbarium:

The facilities of the Harvard University Herbarium and the additional space now available in the Administration Building in Jamaica Plain have afforded the herbarium staff the desired opportunity for expansion and proper organization of the herbarium collections of the Arnold Arboretum. The herbarium in the Administration Building in Jamaica Plain is devoted to specimens of plants under cultivation anywhere in the world, with particular emphasis on those cultivated at Jamaica Plain. These cultivated specimens are supplemented with specimens of spontaneous taxa to allow proper study and determination of the cultigens. The horticultural herbarium was expanded during the past fiscal year to loosen the specimens in each case. The entire herbarium was checked for coverage in relation to such manuals as those by Rehder and Bailey. Specimens needing repairs are being afforded the treatment required in a systematic fashion. The horticultural herbarium has been indexed not only by family but by genus as well, for the convenience of visiting horticulturists. It is of interest to note that during the past year visitors were often interested in either herbarium; but rarely did their work involve both.

The specimens moved to Cambridge were transported in the steel cases or cardboard boxes used to house those specimens in Jamaica Plain. During the year Miss Perry, with the assistance of two student workers, completed the major task of inserting into the steel cases in their proper sequence all specimens formerly contained in cardboard boxes in Jamaica Plain. When this task was completed the long-delayed distribution of recently mounted specimens was begun. Currently the work is also under way to place in proximity the specimens representing families of flowering plants in the herbaria of the Arnold Arboretum and the Gray Herbarium.

During the past year 6,655 specimens were mounted and added to the two herbaria, bringing the total accession count to 681,747 specimens in the herbaria of the Arnold Arboretum. Additional collections and specimens were received, totalling 13,716 numbers. Of these 10,133 were received in exchange and 3,211 by purchase or subsidy of expeditions or collectors. The remainder were received as gifts or in exchange for identifications. Ninety-four percent of the specimens received represented plants from Malaysia, Asia, Africa, Europe and Australia in that order. In recent years the Arnold Arboretum has contributed to the financing of expeditions to New Caledonia, Northern Burma and Kenya Colony. The botanical results of these expeditions are now being made available and the specimens received in terms of subsidy were from these important areas.

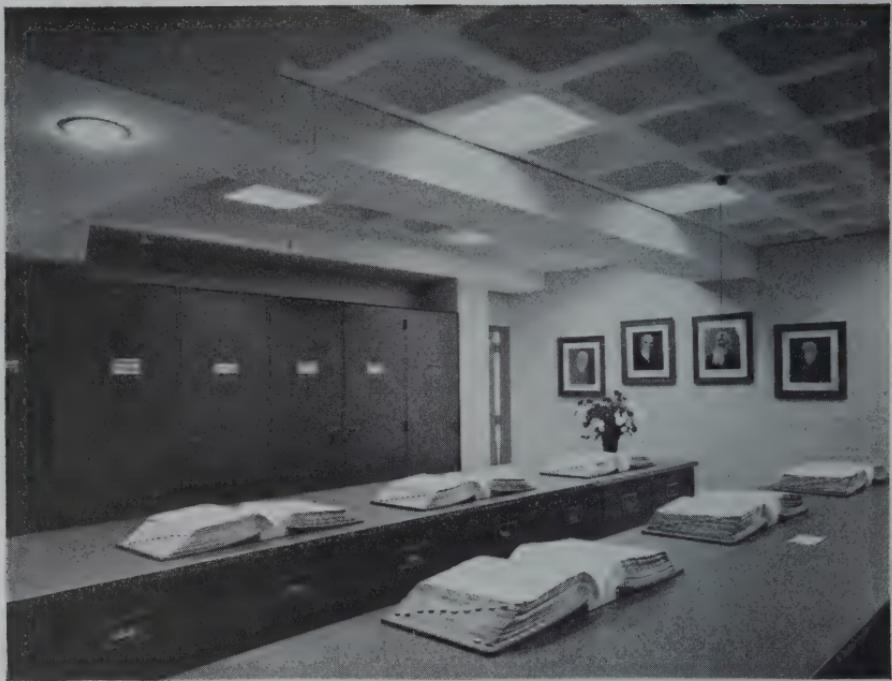


FIG. 4. Top. A portion of the herbarium area in the Harvard University Herbarium. All of the specimens of the Arnold Arboretum are now housed in steel herbarium cases.

FIG. 4. Bottom. A portion of one of the offices for the staff of the Arnold Arboretum in the Harvard University Herbarium. The wall sorting cases for herbarium specimens were specially designed for this building. Recessed lighting throughout the building supplies excellent, evenly-distributed illumination.

Requests for loans of herbarium specimens in the collections of the Arnold Arboretum remained high and in spite of the move in progress, all were handled promptly. Requests were honored for 86 loans to 51 institutions and the loans averaged 130 specimens. The staff feels that the time spent in locating, removing and packing these specimens for shipment to fellow scientists is not only repaid in kind but also enables us to maintain an active herbarium, with specimens determined by specialists. Nevertheless, it is acknowledged that preparing the loans and replacing the sheets in their proper position when the loan is returned is expensive in terms of staff time. The largest number of requests for material on loan came from botanists in the United States, with other requests coming from Europe, Canada, South America, Asia and New Zealand, in order of frequency.

During the year staff members conducted research on plant families and areas of their specialty. Dr. Howard continued his work on the vegetation of bauxite soils in cooperation with the botanists of the Institute of Jamaica, British West Indies. He also was able to devote some time to his studies of petiole structure, the horticultural plants of Florida and the American tropics and to general Caribbean collections.

Dr. Wood made two field trips to the southeastern states and worked on the determination of these plants. He continued his studies of the genus *Hedyosmum* and completed work on *Drosera*.

Dr. Kobuski devoted almost full time to his duties as curator of the herbaria in supervising the work in progress. In addition to his work as editor of the Journal of the Arnold Arboretum, Dr. Kobuski prepared a new edition of a glossary of horticultural terms and continued his studies of the Asiatic members of the Theaceae.

Dr. Johnston taught his course, "Phylogeny and Classification of the Flowering Plants" and devoted the remainder of his time to his research on the Boraginaceae. He gave special attention to the morphology and classification of *Echiochilon* and related genera from the deserts of Africa, Arabia and southern Asia. His studies of the poorly understood genus *Microula* of Tibet and western China are well advanced. He has prepared three long papers on the Boraginaceae for publication.

Dr. Perry devotedly gave her full time to arduous work in the organization of the herbarium. It was largely through her efforts that the specimens housed in cardboard boxes were efficiently transferred to their proper positions in the regular herbarium. In the latter part of the year Miss Perry was able to turn a small part of her attention to her own research interests on the vegetation of New Guinea and she was able to resume her work on the extensive collections of L. J. Brass from Papua.

Dr. Hu, botanist of the Flora of China Project, efficiently supervised the work of Dr. Liu and Dr. Ting. Together they have continued the indexing of Chinese plants and the preparation of a card file to record the Chinese vegetation. Dr. Hu and Dr. Liu together have completed a treatment of the family Malvaceae as it occurs in China.

Comparative Morphology:

During the past year the wood, wood slide and pollen slide collections of the Arnold Arboretum formerly housed in the Biological Laboratories were transferred to the Harvard University Herbarium. These collections occupy a large room on the first floor adjacent to the paleobotanical collections and convenient to the herbarium. Professor Bailey and his assistants completed the necessary rearrangement of materials in the new cases housing these collections. The wood collection is now in the same systematic sequence as the herbarium.

The most valuable additions to the collection in the past year are the specimens secured in Fiji by Dr. A. C. Smith and the specimens of the genus *Coccoloba* collected by Dr. R. A. Howard in the Caribbean Islands. During the year valuable specimens of the woody Compositae were contributed by Mr. Carlquist of the University of California; numerous slides of the Magnoliaceae by Professor Canright of Indiana University and valuable slides of *Garrya* by Professor Moseley of Santa Barbara College.

The wood collection, and particularly the microscope slide collection related thereto, have become increasingly significant in the study of plant relationships and classification and in the identification of fossil woods. In addition, they have rendered a public service in solving problems raised by art museums, archeologists, criminal divisions of the police department, timber users and others.

Cytogenetics:

Dr. Karl Sax, his assistants and students reported the following contributions in the field of cytogenetics. New hybrids of *Forsythia*, *Rhododendron*, *Philadelphus*, *Prunus* and *Malus* developed at the Arnold Arboretum were grown in the nursery in Jamaica Plain and in test plots at the Case Estates in Weston. Four of the best of the apple hybrids which merit distribution have been named in honor of associates of the Arnold Arboretum. These were published in *Arnoldia* and are *Malus* × "Henrietta Crosby," *Malus* × "Blanche Ames," *Malus* × "Henry F. duPont," and *Malus* × "Mary Potter."

An analysis of the relations between aneuploidy and morphological characters among the progeny of triploid *Forsythia* and *Philadelphus* was made by Dexter Sampson.

The various techniques used for producing dwarf fruit trees which have been tested at the Arnold Arboretum in Jamaica Plain and in Weston have now been used to produce dwarf ornamental trees. The use of dwarfing rootstock has given promising results with several species of maple which would be equally desirable as dwarf trees.

Two chemical preparations for use with plant materials have been developed which are proving of interest and value to horticulturists. A compound of 10% weed killer (equal parts of 2,4,5-T and 2,4-D) in a paste of lanolin or similar grease can be used to kill poison ivy growing in among

vines or shrubs without injury to the adjacent plants. A second compound of 10% wettable chlordane in a lanolin or grease base when painted on the trunks of peaches and similar trees effectively controls boring insects. Both compounds will soon be available from commercial sources.

The work on the effects of ionizing radiation, supported by the Atomic Energy Commission, has led to the use of X-rays to promote earlier flowering in certain plant species. Ornamental trees and shrubs from the Arnold Arboretum are being grown in the "gamma field" at Brookhaven, Long Island, for the induction of bud mutations in collaboration with the Brookhaven National Laboratory.

Instruction:

During the year various staff members continued their cooperation with the Department of Biology of the University in presenting formal courses, informal seminars and guiding the work of graduate students. Dr. Ivan Johnston offered an advanced course in plant taxonomy in the spring semester. Dr. Karl Sax continued his guidance of the work of Mr. Dexter Sampson and Julian Jaffee. Mr. Jaffee completed his thesis and received his degree at midyear's. Dr. Richard Howard supervised the graduate work of Miss Siri von Reis on the botanical activities and travels of Erik Ekman and of Mr. Tchang Bok Lee, an UNKRA fellow from Korea who is working on the forests and forest products of Korea. Cooperation was also offered to the School of Landscape Design of Harvard by Dr. Howard, under whose direction several classes studied the plant materials on the grounds of the Arboretum.

Many of the staff members attended and took part in the seminars offered in the field of plant systematics for graduate students and staff at the Harvard University Herbarium. An average of thirty persons attended these weekly seminars, which were conducted throughout the year. Dr. Wood spoke on "Hybridization in *Drosera*"; Dr. Perry on "Plant Exploration in New Guinea"; Dr. Kobuski on "Problems in the Theaceae" and Dr. Howard on "The Use of Anatomical Characters of the Petiole as an Aid to Plant Classification."

Travel and Exploration:

New horticultural introductions as well as herbarium specimens came to the Arboretum through the field efforts of its staff as well as through expeditions by foreign collectors supported by the Arnold Arboretum. Of the staff members, Dr. Howard and Dr. Wood carried on botanical explorations during one trip to southern Florida and the Bimini Island group of the Bahamas in the British West Indies in February. On this trip they collected in the Florida Everglades National Park and visited the Fairchild Tropical Garden, the Kampong (the home of Mrs. David Fairchild), the Coconut Grove Plant Introduction Station of the U.S. Department of Agriculture and the Gifford Arboretum of the University of Miami. In the Bahamas they were guests of the American Museum of Natural History at the Lerner Marine Laboratories where they continued



FIG. 5. Top. Mr. Roger Coggeshall instructing one of the adult education classes in plant propagation held at the greenhouses in Jamaica Plain.

FIG. 5. Bottom. Dr. Donald Wyman (at right, back to camera) discusses the lilac collection of the Arnold Arboretum with members of the Springfield Class of the Adult Education Program.

explorations of those islands begun by Dr. Howard in 1948. In addition to field studies, work was done on the cytology of tropical plants and in anatomical investigations of tropical plant species. Dr. Howard also continued the cooperation between the Arnold Arboretum and the Institute of Jamaica in Kingston, Jamaica, British West Indies. He spent three weeks in September working with the botanists of the Institute in conducting a survey of the vegetation on bauxite soils which are to be mined by several aluminum companies.

In April Dr. Wood traveled and collected in North Carolina, South Carolina and Georgia. He brought back to the Arboretum over fifty living collections, species and hybrids of *Robinia*, the rose acacia, for addition to our living collections or for testing and study in connection with his investigations of that genus. Dr. Wood was also able to obtain living material of *Liquidambar styraciflua* var. *rotundiloba*, named by Dr. Rehder but not currently in the Arboretum's collections.

During the year the Arboretum supported expeditions in Australia, Japan and South America and from these expeditions obtained seeds of ornamental plants for trial in the United States.

Gifts and Grants:

The Arnold Arboretum is fortunate to have the new and renewed financial support of a large group of benefactors known as the Friends of the Arnold Arboretum. The support of our work by these loyal benefactors among whom are many organizations is deeply appreciated by the entire staff. Gifts from the Friends to Harvard University for the purposes of the Arnold Arboretum, unless specified for particular purposes, are assigned to a fund known as Gifts for Cultural Purposes. During the past fiscal year such funds were used to employ additional seasonal labor in the maintenance of the grounds, to carry on experiments in the winter protection of evergreens, particularly rhododendrons, and to afford research assistance to members of the staff for work on horticultural projects.

In addition to these gifts for unrestricted purposes, the Arboretum has received gifts and grants for special research projects and special purposes. The largest of these from the China International Foundation supports the work of three botanists and two secretaries in investigations of the flora of China. Grants from the Stark Brothers Nurseries for the work of Dr. Karl Sax has supported investigations in methods of dwarfing trees by the control of growth. Dr. Sax has also received grants from the atomic energy commission for study in the effects of radiation on cell division and growth and in the transport of materials through the body of plants.

Dr. Carroll Wood received a grant from the American Association for the Advancement of Science through the American Academy of Arts and Sciences for exploration and collection of materials in the Gaspe Peninsula of Canada. This work will be completed during the coming summer months.

A gift for the specific purpose of "repair of hurricane damage" was received from the Association for the Arnold Arboretum, Inc. With the approval of its president and board of directors, this gift was used to pur-

chase a brush chipper and chain saw to facilitate the removal of fallen trees.

A non-departmental gift from Mr. George R. Cooley for taxonomic work at the joint discretion of Dr. Reed Rollins, Director of the Gray Herbarium, and Dr. Richard Howard has been utilized to support field work and research on the vegetation of the southeastern states and the adjacent Caribbean Islands. Travel leading to collections and determinations of the woody ornamental plants under cultivation as well as the native and spontaneous plants of the area has been made possible through this gift.

Gifts in kind, including books for the library as well as herbarium specimens, have been received from many sources. Mr. Harvey Templeton, Jr., kindly presented to the Arnold Arboretum an experimental intermittent mist propagation system which has been erected near the greenhouses. This gift will enable Mr. Coggeshall and others to run comparison tests of rooting techniques on woody plants under the polyethylene plastic and under the intermittent spray system.

The Arboretum is particularly indebted to Mr. and Mrs. F. H. Palmer of Wellesley, Massachusetts, for a gift of 150 bound volumes of books and periodicals from their library, many of these originally in the library of Mr. H. H. Hunnewell. This important gift of volumes in fine bindings not only adds several valuable items to the libraries but gives us a number of reserve copies for volumes in continuous use and receiving wear.

From the trustees of Lingnan University the Arboretum has received a gift of 8058 herbarium specimens representing plants of China. These specimens were borrowed by staff members of the Arboretum prior to the war years and were packed ready to be returned at the outbreak of World War II. As the specimens were being kept apart as a loan to be returned, they could not be studied or cited and were difficult to afford proper care. The trustees of Lingnan University, recognizing the value of these specimens, if accessible, to the work of the Arboretum and other institutions, presented them to be incorporated in the herbarium. The specimens were all stamped with a special imprint recognizing the date of this gift. When it is possible to reestablish botanical work in China at the Lingnan University, the Arboretum will replace this gift with comparable specimens from its collection of duplicates of plants from China.

Publications:

The breadth of interest and the nature of the activities and the contribution of the staff of the Arboretum is always indicated in the bibliography and published writings given at the end of the annual report. I wish, however, to call special attention to the publications of the past year.

The request for out-of-print numbers of articles which appeared in the Bulletin of Popular Information and in Arnoldia led to the reprinting of many of these articles as *The Arnold Arboretum Garden Book*. This book of 354 pages, published by D. Van Nostrand Company, Inc., was edited by Dr. Wyman. It has been widely and favorably reviewed and meets the needs of the public interested in woody trees and shrubs for information on

selection and care of such plants. Dr. Wyman also completed the manuscript and the proofs for a new edition of *Crab Apples for America*, to be published by the American Association of Botanic Gardens and Arborets.

Two other books by staff members were published during the course of the last fiscal year and two others were seen through proofs and will appear shortly.

The Botany of Cook's Voyages, by Dr. E. D. Merrill, was published by Chronica Botanica and appeared in December, 1954. This book is in one regard a summary of many of Dr. Merrill's investigations in the origin and distribution of the plant life of the Pacific Islands.

The Chronica Botanica Company also published a selection of the research papers of Professor I. W. Bailey in December, 1954, under the title of "Contributions to Plant Anatomy." The staff takes pride in the fact that almost all of the papers reprinted in this book appeared in the Journal of the Arnold Arboretum during the course of Professor Bailey's active career.

Dr. Sax completed work on his study of population problems among the world's people and this book entitled, *Standing Room Only* is to be released in July by the Beacon Press.

Mrs. McKelvey is also completing the index to her book, *Botanical Exploration of the Trans-Mississippi West, 1790-1840*, which will be published in the fall.

New brochures describing the activities, resources and personnel of the Arboretum were prepared and have been distributed to garden clubs and in connection with the various open houses held.

Twelve issues of *Arnoldia* were prepared under the editorship of Dr. Wyman. An issue was distributed on September 24th reporting on the hurricane damage and was followed on October 15th by a special number devoted to the "Rehabilitation of Trees Injured by Hurricanes of 1954." In response to many requests for an earlier issue of *Arnoldia*, now out of print, Mr. Coggeshall brought up to date the information on the uses of polyethylene plastic at the Arboretum. Appropriately, at Christmas time Dr. Wyman published a delightful biographical sketch of Wilfrid Wheeler, "the Holly man" and listed with descriptions the best of the fruiting hollies named by Mr. Wheeler. Dr. Karl Sax described the work of the Arboretum staff in the field of plant breeding in the April issue of *Arnoldia*, while other issues appropriate to the season covered the subjects of forcing woody plants for early bloom, lilacs and old fashioned roses.

Four quarterly issues of the Journal of the Arnold Arboretum were published under the editorship of Dr. C. E. Kobuski. The articles in the Journal are more technical in nature. Priority of publication goes to staff members of the Arboretum and, in general, articles by other authors are accepted if they are based on materials in the collections of the Arboretum. Many of the articles dealt with basic investigations in horticultural subjects such as "The Control of Tree Growth by Phloem Blocks" by Dr. Sax, "Polyplodiy and Apomixis in Cotoneaster" by Mrs. Sax, "Induction of Early Flowering of Ornamental Apple Trees" by Karl Sax and Albert

Johnston and "A Monograph of the Genus *Philadelphus*" by Dr. Hu. Other articles, such as "The Cyperaceae Collected in New Guinea by L. J. Brass, IV" and "The Cryptogams of the 1948 Archbold Cape York (Queensland) Expedition," were submitted by specialists who worked on collections made by an Arboretum-sponsored expedition.

The April and July numbers of Volume 36 of the Journal of the Arnold Arboretum were combined in a special issue dedicated to Professor Bailey by the editorial board. All of the papers were prepared at our request by former students and associates of Professor Bailey. The combined number carried the following dedication:

"On the occasion of the retirement of Professor Irving Widmer Bailey, after twenty-two years on the staff of the Arnold Arboretum and forty-seven years of service to Harvard University, we, his associates on the editorial board of the Journal of the Arnold Arboretum, dedicate this issue to him.

"The authors of the articles in this special number of the Journal represent only a few of the students and associates of Professor Bailey who would pay tribute to him at this time. We honor him with this issue in recognition of his contributions, his high standards of research, his integrity in science and personal life, and his guidance of and inspiration to students in the field of botany."

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1954-1955

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INDEX

Acacia, 222
Acanthophippium vitiense, 276
Acmopyle sahniana, 274
Agatea violaris, 284
Agathis vitiensis, 274
Airosperma trichotomum, 288
Alangium villosum vitiense, 285
Alcimandra, 121
Amaracarpus musciferus, 289
Amaranthus gracilis, 226
Amaroria soulameoides, 279
Amyris elemifera, 214, 215, 216, 229
— *granulata*, 217, 221, 229
Andropogon nodosus, 400
Andruris vitiensis, 274
Annona bicolor, 227
Antirrhoea elliptica, 215, 221, 237
— *lucida*, 237
Aristolochia bilobata, 217, 225
Armouria beata, 232
Arnold Arboretum during the Fiscal Year
 Ended June 30, 1955, The. The Director's Report, 403
Aromadendron, 122
Asystasia gangetica, 399
Atriplex pentandra, 225
Aveledoa, 160
Avicennia, 215
— *nitida*, 215, 237

BAILEY, I. W. AND MARGERY P. F. MARDEN. A Fourth Type of Nodal Anatomy in Dicotyledons, Illustrated by *Clerodendron trichotomum* Thunb., 1

BAILEY, IRVING WIDMER. Portrait, Dedication, Nos. 2 & 3, i

Balanops vitiensis, 277

Bambusa sp., 400

BARGHOORN, ELSO S. AND RICHARD A. SCOTT. The Occurrence of *Euptelea* in the Cenozoic of Western North America, 259

Batis, 216
— *maritima*, 226

Begonia vitiensis, 285

Berrya pacifica, 283

Bibliography of the Published Writings of the Staff and Students, July 1, 1954—June 30, 1955, 428

Boerhaavia caribaea, 226

Boronella Baill., Comparative Morphology of the Foliar Sclereids in, 189

Boronella crassifolia, 190
— *francii*, 190
— *pancheri*, 190
— *verticillata*, 190
Borreria arborescens, 215, 238
Bourreria maritima, 237
Brackenridgea nitida, 284
Broughtonia domingensis, 224
Brucea quercifolia, 280
Bumelia, 222
Buraeavia horneana, 280
Bursera simaruba, 216, 229

Cactus lemari, 220, 233
Caesalpinia anacantha, 214, 216, 227
— *ciliata*, 227
— *glandulosa*, 228
Cakile lanceolata, 227
Calamus vitiensis, 274
Calonyction tuba, 214, 236
Calypptosepalum pacificum, 277
Cameraria angustifolia, 216, 235
Canavalia maritima, 214, 228
Canella alba, 214, 233

CANRIGHT, JAMES E. The Comparative Morphology and Relationships of the Magnoliaceae — IV. Wood and Nodal Anatomy, 119

Capparis cynophallophora, 220, 227
— *flexuosa*, 214, 217, 220, 227

Cardiopteris, 161

Cardiospermum corindum, 231

Carruthersia latifolia, 287
— *scandens*, 287

Casearia, 222

Cassia buchii, 214, 228
— *leschenaultiana*, 398
— *strigillosa*, 214, 228

Cassytha americana, 227

Cayratia acuminata, 282
— *seemanniana*, 282

Celosia nitida, 226

Celtis trinervia, 224

Cenchrus brownii, 222
— *myosuroides*, 222
— *pauciflorus*, 214, 222

Cephalocereus polygonus, 216, 233

Chascotheca domingensis, 230

CHEADLE, VERNON I. The Taxonomic Use of Specialization of Vessels in the Metaxylem of Gramineae, Cyperaceae, Juncaceae, and Restionaceae, 141

Chiococca alba, 217, 237
Chloris inflata, 400
Chroniochilus godeffroyanus, 276
Chrysoglossum gibbsiae, 276
 — *vesicatum*, 276
Cissus, 217
 — *caustica*, 232
 — *fuertesii*, 232
 — *macilenta*, 232
 — *micrantha*, 232
 — *trifoliata*, 232
Citharexylum fruticosum, 237
Cleidion leptostachyum, 281
Cleistanthus micranthus, 280
Cleistocalyx, 285
Clematis pickeringii, 277
Clerodendron trichotomum Thunb., A
 Fourth Type of Nodal Anatomy in
 Dicotyledons, Illustrated by, 1
Clerodendron spinosum, 215, 237
Clidemia hirta, 398
Cloëzia microphylla, 286
Clusea rosea, 217, 233
Coccinea cordifolia, 398
Coccoboa diversifolia, 216, 225
 — *pubescens*, 216, 221, 225
 — *subcordata*, 225
 — *uvifera*, 221, 225
 — — *× C. pubescens*, 225
Colubrina ferruginea, 214, 231
 — *reclinata*, 232
Commelinia diffusa, 217, 224
Comocladia dodonea, 216, 217, 230
 — *mollifolia*, 216, 217, 230
 Comparative Morphology of the Foliar
 Sclereids in *Boronella Baill.*, 189
 Comparative Morphology and Relation-
 ships of the Magnoliaceae — IV. Wood
 and Nodal Anatomy, The, 119
Connarus pickeringii, 279
Conocarpus erecta, 215, 234
 — — *sericea*, 234
Corchorus hirsutus, 214, 232
Cordia buchii, 217, 236
Cossignia pacifica, 282
Couthovia, 287
Croton lucidus, 229
 — *polytomus*, 229
Cryptorhiza haitiensis, 216, 234
Cryptostylis vitiensis, 276
Cyathocalyx, 278
Cyclura cornuta, 215
Cynoglossum amabile, 399
Cynometra falcata, 279
 — *insularis*, 279
 Cyperaceae, Juncaceae, and Restionaceae,
 The Taxonomic Use of Specialization
 of Vessels in the Metaxylem of Grami-
 neae, 141
Cyperus compressus, 220, 223
 — *nanus*, 215, 223
 — *planifolius*, 215, 223
Dacrydium elatum, 274
 — *lycopodioides*, 274
Dactylis glomerata, 400
 DAHL, A. ORVILLE. The Pollen Morphol-
 ogy of Several Genera Excluded from
 the Family Iacinaeae, 159
Deeringia amaranthoides, 277
Degeneria, 277
Desmanthus virgatus, 228
Desmodium triflorum, 228
Desmos insularis, 278
 — *leucanthus*, 278
Deutzia chanetii, 93
 — *corymbosa*, 365
 — *gracilis*, 365
 — *japonica*, 365
 — *mollis erythrocalyx*, 346
 — *pulchella*, 365
 — *sanguinea*, 58, 365
 — *thrysiflora*, 365
 — *undulata*, 365
 Dicotyledons, Illustrated by *Clerodendron*
trichotomum Thunb., A Fourth Type
 of Nodal Anatomy in, 1
 Differentiation of Xylem, On the, 305
Dillenia biflora, 284
Dolicholobium, 288
Drimys insipida, 389
 — *lanceolata*, 389
 — *purpurascens*, 389
 — *stipitata*, 389
 — *vickeriana*, 389
Drypetes vitiensis, 280
Durandea vitiensis, 279
Duranta repens, 220, 237
Dyschoriste repanda, 287
 EAMES, ARTHUR J. The Seed and Ginkgo,
 165
 Early Flowering of Ornamental Apple
 Trees, Induction of, 110
Echites umbellata, 214, 236
Elaeodendron ehrenbergii, 221, 231
 — *vitiense*, 281
 — *xylocarpum*, 217, 231
Elatine gratioloides, 284
Eleutheranthera ruderalis, 398
Elmerrillia, 122
Endospermum macrophyllum, 281
 — *robbieanum*, 281
Ephedra alata, 243

Ephedra altissima, 243
 — *californica*, 243
 — *chilensis*, 243
 — *equisetina*, 243
 — *gerardiana*, 243
 — *intermedia*, 243
 — *major procera*, 243
 — *viridis*, 243
Erigeron albidus, 399
 — *floribundus*, 399
 — *sumatrensis*, 399
Eriochloa procera, 400
Erithalis vaccinifolia, 215, 238
Ernodea littoralis, 215, 238
Erythroxylon areolatum, 228
Eugenia aeruginea, 235
 — *buxifolia*, 235
 — *fragrans*, 235
 — *linearis*, 235
 — *rhombea*, 235
Eulophia, 276
Eupatorium corymbosum, 220, 238
Euphorbia australis, 399
 — *buxifolia*, 229
 — *drummondii*, 399
 — *hepatica*, 217, 221, 230
Eupomatia, 386
 — *bennettii*, 386, 388, 390, 392
 — *laurina*, 386, 388, 391, 393
Eupomatiaceae, Geographical Distribution of the, 385
Euptelea in the Cenozoic of Western North America, The Occurrence of, 259
Euptelea baileyana, 260
Evolvulus alsinoides, 214
 — — *grisebachianus*, 236
Exorrhiza vaupelii, 275
Exostemma caribaeum, 217, 238

Factors in Pollen Germination: Calcium Salts, Dextrose, Drying, Some, 171

FAULL, ANNA F. Some Factors in Pollen Germination: Calcium Salts, Dextrose, Drying, 171

Ficus populnea, 220
 — — *hispaniolae*, 216, 224

Fiji, Further Notes on the Weeds and Introduced Plants of, 397

Fiji, Phanerogam Genera with Distributions Terminating in, 273

Fimbristylis spathacea, 220, 223

Firmiana diversifolia, 283

Forsythia, Studies on the Progeny of Triploid *Philadelphus* and, 369

Forsythia intermedia, 374

FOSTER, ADRIANCE S. Comparative Morphology of the Foliar Sclereids in *Boronella Baill.*, 189

FRISBIE, LEONARD F. *Rhododendron macrophyllum* D. Don ex G. Don, 115

Fruit Size, Stalk Diameter as a Factor in, 267

Frutex coronarius, 99

Further Notes on the Weeds and Introduced Plants of Fiji, 397

Galactia dictyophylla, 217, 221, 228

Geissois, 278

Geographical Distribution of the Eupomatiaceae, 385

Gillespiea speciosa, 289

Ginkgo, The Seed and, 165

Gmelina vitiensis, 287

Goniocladus petiolatus, 275

Goniosperma thurstonii, 275
 — *vitiensis*, 275

Gonostylus punctatus, 285

Gossypium hirsutum punctatum, 232
 — spp., 398

Gramineae, Cyperaceae, Juncaceae, and Restionaceae, The Taxonomic Use of Specialization of Vessels in the Metaxylem of, 141

Grammatophyllum elegans, 276

GRAY, NETTA E. A Taxonomic Revision of *Podocarpus*. IX. The South Pacific Species of Section *Eupodocarpus*, Sub-section F, 199

GREENWOOD, WILLIAM. Further Notes on the Weeds and Introduced Plants of Fiji, 397

Guaiacum sanctum, 229

Guettarda stenophylla, 216, 217, 221, 238
 — *xanthocarpa*, 216, 217, 221, 238

Gymnanthes lucida, 230

Gymnema stenophyllum, 287
 — *subnudum*, 287

Haitiella ekmanii, 215, 216, 224

Hedstromia latifolia, 289

Hibbertia lucens, 283
 — *scandens*, 389
 — *volubilis*, 389

Himantandra belgraveana, 386

Hippomane manchinella, 230
 — *spinosa*, 216, 230

Hiptage myrtifolia, 280

HOTCHKISS, A. T. Geographical Distribution of the Eupomatiaceae, 385

HOWARD, RICHARD A. The Vegetation of Beata and Alta Vela Islands, Hispaniola, 209

HU, SHIU-YING. A Monograph of the Genus *Philadelphus*, 52, 325

Hydnophytum, 289

Hydrilla verticillata, 399

Icacinaeae, The Pollen Morphology of Several Genera Excluded from the Family, 159

Indigofera suffruticosa, 214, 228

Induction of Early Flowering of Ornamental Apple Trees, 110

Ipomoea acuminata, 236

— *eriosperma*, 236

— *pes-caprae*, 214, 236

— *tiliacea*, 236

Iresine angustifolia, 220, 226

Isidorea leonardii, 216, 217, 238

Jacquemontia jamaicensis, 236

Jacquinia barbasco, 214, 235

— *linearis*, 235

Jatropha hernandifolia, 216, 230

— *multifida*, 230

JOHNSON, ALBERT G. AND KARL SAX. Induction of Early Flowering of Ornamental Apple Trees, 110

Juncaceae, and Restionaceae, The Taxonomic Use of Specialization of Vessels in the Metaxylem of Gramineae, Cyperaceae, 141

Kermadecia ferruginea, 277

— *vitiensis*, 277

Kingiodendron platycarpum, 279

Kmeria, 123

Koelreuteria elegans, 282

Krugiodendron ferreum, 217, 232

Laeliopsis domingensis, 224

Laguncularia, 215

— *racemosa*, 234

Lantana reticulata, 214, 237

Leucopogon cymbulae, 286

Lindenia vitiensis, 288

Liriodendron, 123

Lithophila muscoides, 215, 220, 226

Lochnera rosea, 236

Lophophyxis, 160

— *pentaptera*, 160

Magnolia, 124

Magnoliaceae, The Comparative Morphology and Relationships of the — IV. Wood and Nodal Anatomy, 119

Malpighia domingensis, 216, 217, 229

— *setosa*, 216, 217, 229

Manglietia, 125

Mariscus bruneus, 223

MARSDEN, MARGERY P. F. AND I. W. BAILEY. A Fourth Type of Nodal Anatomy in Dicotyledons, Illustrated by *Clerodendron trichotomum* Thunb., 1

MARSDEN, MARGERY P. F. AND TAYLOR A. STEEVES. On the Primary Vascular System and the Nodal Anatomy of *Ephedra*, 241

Mastixiodendron, 288

Maytenus, 222

— *reynosoides*, 231

Melochia tomentosa, 233

Mesechites repens, 217, 236

Metaxylem of Gramineae, Cyperaceae, Juncaceae, and Restionaceae, The Taxonomic Use of Specialization in the, 141

Metopium brownei, 216, 231

— *toxiferum*, 216, 231

Metteniusa, 160

— *nucifera*, 160

— *tessmanniana*, 160

Michelia, 125

Microcos vitiensis, 283

Mimosa, 222

Mitochondria and Precipitates of A-type Vacuoles in Plant Cells, 293

Monograph of the Genus *Philadelphus*, A, 52, 325

Mooria microphylla, 286

Morinda roycoc, 220, 238

Neea subcoccinea, 226

Nealsomitra integrifoliola, 289

Neoveitchia storckii, 274, 275

Nodal Anatomy in Dicotyledons, Illustrated by *Clerodendron trichotomum* Thunb., A Fourth Type of, 1

Nodal Anatomy of *Ephedra*, On the Primary Vascular System and the, 241

Nodal Anatomy. The Comparative Morphology and Relationships of the Magnoliaceae — IV. Wood and, 119

Nymphaea capensis, 397

— — *rosea*, 398

Oncidium intermedium, 224

Opuntia antillana, 220, 233

— *caribaea*, 234

— *dillenii*, 214, 220, 234

— *moniliformis*, 216, 217, 234

Ornamental Apple Trees, Induction of Early Flowering of, 110

Pachygone vitiensis, 277

Pagiantha koroana, 287

Pagiantha thurstonii, 287
Panicum adsperrum, 222
 — *maximum*, 214, 222
Paphia vitiensis, 286
Parkia parii, 279
Parsonia laevis, 287
Paspalum adspersum, 220
 — *bakeri*, 220, 222
Passiflora suberosa, 214, 233
Paullinia jamaicensis, 217, 231
Peripterygium, 161
 — *moluccanum*, 161
Phanerogam Genera with Distributions Terminating in Fiji, 273
Philadelphus and Forsythia, Studies on the Progeny of Triploid, 369
Philadelphus, A Monograph of the Genus, 52, 325
Philadelphus sect. *Coronarii*, 87, 92, 362
 — sect. *Pauciflorus*, 52
 — sect. *Stenostigma*, 52, 68
 — ser. *Coronarii*, 87, 92, 98, 362
 — ser. *Corticatae*, 52, 68
 — ser. *Decorticatae pauciflorae*, 52
 — ser. *Decorticatae racemosae*, 52, 68
 — ser. *Delavayani*, 325
 — ser. *Gordoniani*, 70, 332
 — ser. *Pekinenses*, 92
 — ser. *Pubescentes*, 332
 — ser. *Satsumani*, 362
 — ser. *Sericanthi*, 336
 — ser. *Speciosi*, 53
 — ser. *Tomentosii*, 87
 — subg. *Euphiladelphus*, 52
 — subsect. *Coronarii*, 92, 98
 — subsect. *Gemmatae*, 325
 — subsect. *Gordoniani*, 70, 332
 — subsect. *Satsumani*, 87, 325, 362
 — subsect. *Speciosi*, 52
 — *acuminatus*, 365
 — *amurensis*, 361
 — *angustifolius*, 79
 — *aromaticus*, 99
 — "Belle Etoile," 369
 — "Bicolore," 369, 370
 — *brachybotrys*, 95
 — — *laxiflorus*, 96
 — — *purpurascens*, 330
 — *caucasicus*, 106
 — — *aureus*, 108
 — — *glabratus*, 107
 — *chinensis*, 364
 — *cineratus*, 347
 — *coloratus*, 106
 — *columbarius myrtiflorus*, 63
 — *columbiensis*, 58, 76
 — *confusus*, 86
 — *cordatus*, 63, 76
 — — *cordifolius*, 63
 — — *Coronarii*, 69, 70, 332
 — — *coronarius*, 98
 — — — *acuminatus*, 365
 — — — *aureus*, 108
 — — — *chinensis*, 343
 — — — *cochleatus*, 103
 — — — *deutziaeflorus*, 102
 — — — *dianthiflorus*, 103
 — — — *duplex*, 101
 — — — *flore plena*, 101
 — — — *fol. argenteo-marginatis*, 106
 — — — *fol. aureis*, 108
 — — — *genuinus*, 99
 — — — *mandshuricus*, 361
 — — — *multiflorus plenus*, 102, 105
 — — — *nanus*, 101
 — — — *nivalis*, 63, 72
 — — — *pekinensis*, 93
 — — — *plenus*, 105
 — — — *primulaeflorus*, 104, 105
 — — — *plenus*, 105
 — — — *pumilus*, 101
 — — — *rosaeflorus plenus*, 105
 — — — *salicifolius*, 109
 — — — *satsumanus*, 363
 — — — *satsumi*, 358, 364
 — — — *tenuifolius*, 348
 — — — *tomentosus*, 88, 338
 — — — *variegatus*, 106
 — — — *vulgaris*, 99
 — — — *zeyheri*, 104
 — — *dasycalyx*, 341
 — — *delavayi*, 325
 — — *calvescens*, 330
 — — *cruciflorus*, 329
 — — *melanocalyx*, 328
 — — *trichocladus*, 329
 — — *deyrolleanus*, 99
 — — *discolor*, 333
 — — *dubius*, 333
 — — *flore albo majore inodoro*, 56
 — — *floribundus*, 63
 — — *floridus*, 65
 — — — *faxonii*, 67
 — — — *rehderianus*, 68
 — — *gattingeri*, 336
 — — *globosus*, 72
 — — *gloriosus*, 58
 — — *gordonianus*, 76
 — — — *columbianus*, 76
 — — — *parviflorus*, 363
 — — *grahami*, 63, 76
 — — *Grandiflori*, 53
 — — *grandiflorus*, 58, 333
 — — *floribunda*, 333

Philadelphus grandiflorus laxus, 61
 — *helleri*, 79
 — *henryi*, 346
 — — *cinereus*, 347
 — — *lissocalyx*, 330
 — *humilis*, 61
 — *hupehensis*, 361
 — *ignea*, 61
 — *incanus*, 338
 — — *baileyi*, 340
 — — *sargentianus hupehensis*, 361
 — — — *kulingensis*, 345
 — *inodorus*, 55
 — — *carolinus*, 63
 — — *grandiflorus*, 58
 — — — *quadrangleliflorus*, 61
 — — *laxus*, 61
 — — *strigosus*, 64
 — *intectus*, 82
 — — *pubigerus*, 84
 — *intermedius*, 81
 — *japonicus*, 365
 — *kansuensis*, 356
 — *keteleeri*, 105
 — *kochianus*, 99
 — *lancifolius*, 91
 — *lasiogynus*, 360
 — *latifolius*, 333
 — — *pubescens*, 333
 — — *laxiflorus*, 97
 — — *laxus*, 61
 — — *strigosus*, 64
 — *ledebourii*, 365
 — *lewisii*, 71
 — — *angustifolius*, 79
 — — *ellipticus*, 81
 — — *gordonianus*, 75
 — — *helleri*, 79
 — — *intermedius*, 81
 — — *oblongifolius*, 78
 — — *parvifolius*, 77
 — — *platyphyllus*, 78
 — *macranthus*, 58
 — *magdalenae*, 343, 355
 — *mandshuricus*, 361
 — *matsumuranus*, 363
 — *mitsai*, 342
 — *multiflorus*, 63
 — *nanus*, 101
 — *nepalensis*, 88, 89, 330, 346, 364
 — *nipaulensis*, 88
 — *nivalis*, 72
 — *oreganus*, 85
 — *pallidus*, 99
 — *paniculatus*, 351
 — *parviflorus*, 93
 — *pekinensis*, 93, 365

Philadelphus pekinensis brachybotrys, 95
 — — *dasycalyx*, 341
 — — *kansuensis*, 356
 — — *lanceolatus*, 95
 — — *laxiflorus*, 96
 — — *platyphyllus*, 78
 — — *primulaeflorus*, 105
 — — *pubescens*, 62, 332
 — — — *intectus*, 82
 — — — *verrucosus*, 335
 — — *pulchellus*, 365
 — — *purpurascens*, 330
 — — — *venustus*, 331
 — — *purpureo-maculatus*, 369
 — — *reevesianus*, 340
 — — *rhombifolius*, 335
 — — *robustus*, 348
 — — *roylei*, 364
 — — *rubricaulis*, 93
 — — *salicifolius*, 109
 — — *salzmanni*, 99
 — — *sanguineus*, 82
 — — *satsumanus*, 363
 — — — *nikoensis*, 363
 — — *satsumi*, 364
 — — — *nikoensis*, 365
 — — — *yokohama*, 363
 — — *satzumi schrenkii*, 358
 — — *schrenkii*, 357
 — — — *canescens*, 358
 — — — *jackii*, 360
 — — — *longipedicellatus*, 358
 — — — *mandshuricus*, 361
 — — *sericanthus*, 343
 — — — *kulingensis*, 345
 — — — *rehderianus*, 345
 — — — *rockii*, 343
 — — — *rosthornii*, 343
 — — *shikokianus*, 368
 — — *sinensis*, 368
 — — *speciosus*, 58, 364
 — — *strigosus*, 64
 — — *subcanus*, 351
 — — — *dubius*, 354
 — — — *magdalenae*, 355
 — — — *wilsonii*, 351
 — — “*Sybille*,” 369
 — — *tenuifolius*, 348
 — — — *dentata*, 348
 — — — *latipetalus*, 351
 — — — *multiflorus*, 348
 — — — *schrenkii*, 358
 — — — *subinteger*, 348
 — — — *thrysiflorus*, 72
 — — — *tomentosus*, 88
 — — — *trichothecus*, 84
 — — — *triflorus*, 89, 99

Philadelphus venustus, 331
 — *verrucosus*, 335
 — *viksnei*, 348
 — *wilsonii*, 351
 — *yokohama*, 363
 — *zelleri*, 87
 — *zeyheri*, 104
 — — *kochianus*, 99
 — — *multiflorus*, 63
Phyllostylon, 222
Picroidendron macrocarpum, 216, 229
Pilea, 222
Piliocalyx wagapensis, 285
Pimia rhamnoides, 283
Pithecellobium unguis-cati, 220, 228
 Plant Cells, Mitochondria and Precipitates of A-type Vacuoles in, 293
Plerandra, 286
Plumeria obtusa, 217, 236
Podocarpus, A Taxonomic Revision of. IX. The South Pacific Species of Section *Eupodocarpus*, Subsection F, 199
Podocarpus decipiens, 204
 — *decumbens*, 202
 — *longefoliolatus*, 201
 Pollen Germination: Calcium Salts, Dextrose, Drying, Some Factors in, 171
 Pollen Morphology of Several Genera Excluded from the Family Icacinaceae, The, 159
Polyalthia, 278
Portulaca oleracea, 220, 227
 — *phaeosperma*, 227
 Precipitates of A-type Vacuoles in Plant Cells, Mitochondria and, 293
Pseudobotrys, 159
 — *cauliflora*, 160
Psychotria nutans, 238
Pteleocarpa, 160
 — *malaccensis*, 160
Pterocymbium oceanicum, 283
Ptychosperma, 275
Pullea perryana, 278

Randia parvifolia, 216, 217, 238
Readea membranacea, 289
Remirea maritima, 215, 223
 Report, The Director's. The Arnold Arboretum during the Fiscal Year Ended June 30, 1955, 403
 Restionaceae, The Taxonomic Use of Specialization of Vessels in the Metaxylem of Gramineae, Cyperaceae, Juncaceae, and, 141
Reynosia cuneifolia, 216, 217, 232
Rhacomia crossoptetalum, 215, 231
Rhamnella vitiensis, 282
Rhizophora, 215
 — *mangle*, 234
Rhododendron californicum, 115, 116
Rhododendron macrophyllum D. Don ex G. Don, 115
 — *macrophyllum album*, 117
Richella monosperma, 278
Rinorea storckii, 284
Rivina humilis, 226
Rousselia humilis, 225

Salacia pachycarpa, 281
 — *vitiensis*, 281
Salicornia, 216
 — *bigelovii*, 221, 225
 SAMPSON, DEXTER R. Studies on the Progeny of Triploid *Philadelphus* and *Forsythia*, 369
Samyda pubescens, 217, 233
Sapindus saponaria, 231
Sarcanthus nagarensis, 276
Sarcomphalus domingensis, 216, 232
Sauraia rubicunda, 284
 SAX, KARL AND ALBERT G. JOHNSON. Induction of Early Flowering of Ornamental Apple Trees, 110
Schaefferia frutescens, 231
Schoepfia obovata, 217, 225
 Sclereids in *Boronella Baill.*, Comparative Morphology of the Foliar, 189
 SCOTT, RICHARD A. AND ELSO S. BARGHOORN. The Occurrence of *Euptelea* in the Cenozoic of Western North America, 259
Securinega acidoton, 216, 217, 230
 — *neopeltandra*, 217, 230
 Seed and *Ginkgo*, The, 165
Semecarpus vitiensis, 281
Sesbania sericea, 220, 228
Sesuvium, 216
 — *portulacastrum*, 214, 220, 227
Setaria geniculata, 220, 223
 — *setosa*, 217, 223
Sida acuta, 232, 398
Sideroxylon, 222
 SINNOTT, EDMUND W. Stalk Diameter as a Factor in Fruit Size, 267
 SMITH, A. C. Phanerogam Genera with Distributions Terminating in Fiji, 273
Smythea lanceata, 282
 SOROKIN, HELEN P. Mitochondria and Precipitates of A-type Vacuoles in Plant Cells, 293
 SOROKIN, SERGEI AND RALPH H. WETMORE. On the Differentiation of Xylem, 305

Soulamea amara, 280
Specialization of Vessels in the Metaxylem of Gramineae, Cyperaceae, Juncaceae, and Restionaceae, The Taxonomic Use of, 141
Sporobolus domingensis, 223
— *pyramidalis*, 223
Squamellaria imberbis, 289
— *wilsonii*, 289
Stachytarpheja jamaicensis, 214, 237
Staff of the Arnold Arboretum 1954-1955, 431
Stalk Diameter as a Factor in Fruit Size, 267
STEEVES, TAYLOR A. AND MARGERY P. F. MARSDEN. On the Primary Vascular System and the Nodal Anatomy of *Ephedra*, 241
Stegnosperma cubense, 214, 217, 226
— *halimifolium*, 226
Stigmaphyllum lingulatum sericans, 229
Stillingia pacifica, 281
Storckia vitiensis, 279
Strombus gigas, 216
Strumpfia maritima, 215, 238
Strychnos vitiensis, 287
Studies on the Progeny of Triploid *Philadelphus* and *Forsythia*, 369
Sukunia pentagonioides, 288
Suriana maritima, 214, 216, 229
Symplocos leptophylla, 287
— *turrilliana*, 287
Syringa inodora, 56
— *suaveolens*, 99

Tabebuia ostenfeldii, 217, 221, 237
Talauma, 126
Talinum paniculatum, 220, 227
Tapeinosperma, 286
Taveunia trichospadix, 275
Taxonomic Revision of *Podocarpus*, A. IX. The South Pacific Species of Section *Eupodocarpus*, Subsection F, 199
Taxonomic Use of Specialization of Vessels in the Metaxylem of Gramineae, Cyperaceae, Juncaceae, and Restionaceae, The, 141
Tephrosia cinerea, 214, 228

Tetranthus cupulatus, 238
Tetrastigma vitiensis, 283
Thalassia testudinum, 222
Thespesia populnea, 216, 232
Thunbergia grandiflora, 399
Tillandsia balbisiana, 223
— *circinnata*, 223
— *recurvata*, 223
— *usneoides*, 223
— *utriculata*, 224
Trema, 222
Tribulus cistoides, 229
— *terrestris*, 398
Trichadenia, 161
— *philippensis*, 161
Trichilia cuneifolia, 216, 217, 229
Triploid *Philadelphus* and *Forsythia*, Studies on the Progeny of, 369
Tristania vitiensis, 286
Turnera ulmifolia, 233

Ulbrichia beatensis, 217, 221, 232

Vascular System and the Nodal Anatomy of *Ephedra*, On the Primary, 241
Vegetation of Beata and Alta Vela Islands, Hispaniola, The, 209
Veitchia joannis, 275
— *storkii*, 274, 275
Ventilago vitiensis, 282
Vitiphoenix, 275

Waltheria americana, 233
Wenzelia kambarae, 279
WETMORE, RALPH H. AND SERGEI SOROKIN. On the Differentiation of Xylem, 305
Wood and Nodal Anatomy, The Comparative Morphology and Relationships of the Magnoliaceae — IV., 119
Wormia, 284

Xanthophytum calycinum, 288
Xylem, On the Differentiation of, 305
Xylopia, 278

Zanthoxylum, 222
Zephyranthes bifolia, 217, 224

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